THE
STRUCTURE AND DEVELOPMENT
OF THE FUNGI

PALEOMYCES ASTEROXYLI

from the Old Red Sandstone, Muir of Rhynie, Aberdeenshire, × 100;
after Kidston and Lang

THE
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BY

H. C. I. GWYNNE-VAUGHAN
D.B.E., LL.D., D.Sc., F.L.S.
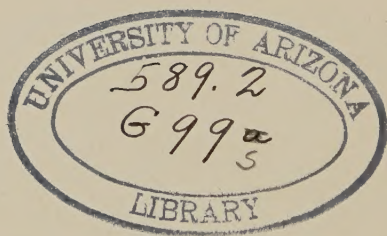*Professor of Botany in the University of London*

AND

B. BARNES
B.Sc., F.L.S.
Lecturer in Botany, Birkbeck College,
University of London

To

THE STUDENTS OF
THE DEPARTMENT OF BOTANY
BIRKBECK COLLEGE

PREFACE

THIS book is in some sense a development of the volume on Fungi prepared by one of us and published in 1922 in the series of Cambridge Botanical Handbooks, for the text and figures have been freely drawn upon and the material revised and brought up to date. But it is also a new book; it includes the whole of the Fungi, not merely selected classes, and it is addressed to the student rather than to the investigator, with the consequence that the material has been somewhat abbreviated. It has been designed to meet the need for such a textbook in our own Department, and we hope it may be equally useful elsewhere.

Most of the illustrations are from published researches, and we desire to thank those authors whose figures we have copied. Illustrations the source of which is not stated are original. In the case of original figures the magnification and the authority for the specific name are given; this has also been done in other cases when the information was available.

We have appended a bibliography which makes no attempt to be exhaustive, it is rather a selection from mycological literature, and we have referred page by page to the relevant papers. There is a vast literature of pathology which we have left almost untouched, it is fully dealt with elsewhere; we are concerned primarily with the fungus, and only secondarily with its effect on other organisms.

It is a pleasure to express our indebtedness to several of our colleagues and to past and present students for specimens and information, and especially to those whose research or suggestions have helped us in the preparation of this book; wherever possible we have acknowledged their help in the text.

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H. C. I. GWYNNE-VAUGHAN
B. BARNES

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INTRODUCTION

The Fungi are saprophytic or parasitic Thallophyta entirely devoid of chlorophyll, reproduced by spores which may be sexual in origin, and possessing, in the great majority of cases, a vegetative portion, or **mycelium**, made up of colourless filaments, or **hyphae**. The origin is remote; the earliest undoubted fungi are found in the Old Red Sandstone; this material (frontispiece)[1] consists of septate hyphae and of vesicles which doubtless served the purpose of reproduction.

Fungal hyphae may be aseptate and coenocytic, or they may undergo transverse septation, in which case their constituent cells are either uninucleate or multinucleate; any division other than transverse[2] is rare. In most cases the hyphae are richly branched; they elongate by apical growth[3], and, as a rule, spread loosely through the substratum; in some cases, and especially in relation to the fruit bodies of higher forms, they become woven into a dense mass which in section gives the appearance of a tissue, and is therefore described as **pseudoparenchymatous**; such a mass, when not forming part of a single fructification, is termed a **stroma**; a similar weft of hyphae may give rise to root-like strands known as **rhizomorphs**, or to a compact resting body, the **sclerotium**, the outer cells of which are modified to form a rind, protecting the mycelium against desiccation.

The mycelium begins its development as a germ tube put out from one of the numerous varieties of fungal spore; where the spore wall is very thin, as in germinating zoospores, the wall of the germ tube is continuous with it, but in most cases the wall of the germ tube is continuous only with the inner layer of the spore wall. One or more germ tubes may push through the wall of the spore at points not previously recognisable, or they may find exit through special pits, the germ pores. The germ tube elongates and receives the contents of the spore.

In certain Archimycetes and in the yeasts, where a mycelium is not developed, the plant consists entirely of reproductive structures.

[1] Kidston and Lang, 1921. [2] Nichols, 1896; Kempton, 1919.
[3] de Bary, 1887; Smith, J. H., 1923.

In most fungi frequent anastomoses take place between adjacent hyphae by means of loops or branches which, when short and straight, are known as **H-pieces**. These may connect not only branches of the same origin, but un-related germ tubes or older filaments (figs. 1, 2); sclerotia or fructifications grown under natural conditions may accordingly be compound structures and the product of two or more spores. Such fusions are presumably nutritive in origin, and result in a pooling of the resources of several spores. Cells

Fig. 1. *Lachnea* sp.; six conidia, the germ tubes of which have undergone fusion, × 720.

of the same hypha are sometimes brought into communication by means of anastomosing branches (fig. 2), which, when they originate as a short, downwardly directed passage between the

Fig. 2. *Phoma* sp.; vegetative hyphae showing anastomoses, × 320. E. Green del.

apical cell of a filament and the cell immediately below (fig. 3), are known as **clamp connections**; they are very common among Autobasidiomycetes and appear there to fulfil a special function. Their nutritive significance, if any, is limited by the fact that the passage is early closed[1].

The fungal protoplast consists of granular or reticulate cyto-plasm, which, in the older regions, leaves a vacuole in the middle

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[1] Hoffmann, 1856, p. 156; Brefeld, 1877 i, p. 17; and cf. p. 246.

of the cell or filament; the nucleus, where its size permits of a detailed study, has a structure similar to that of other plants or animals, and usually divides by mitosis, showing a well-marked spindle with centrosomes and asters; the origin of the spindle is usually intranuclear, but it is extranuclear in the rusts. One or more nucleoli are commonly present; they are thrown into the cytoplasm during karyokinesis and there disintegrate. The extrusion of chromatin bodies has been described.

The cell wall is usually of cellulose; often a special variety known as fungal cellulose is present. The storage materials include oil, protein substances, a dextrose termed soluble starch, amyloid and mannane, both of which give a blue coloration with iodine, and glycogen, which is a carbohydrate readily transformed into sugars.
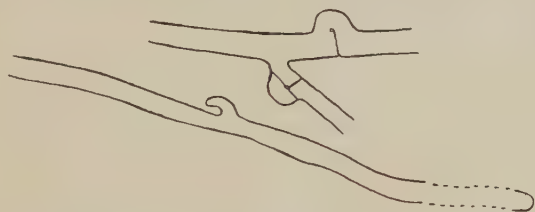
Fig. 3. *Coprinus lagopus* Fr.; clamp connections, × 1065.
E. Green del.

The protoplast also gives rise to a number of ferments which not only enable the fungus to deal with its food materials, but help to break down the host tissues and so make possible the penetration of parasitic hyphae.

Sexual Reproduction among fungi involves the union of the contents of two uninucleate or multinucleate gametangia which may be similar in structure and behaviour or may be differentiated as an antheridium and oogonium. Each of these organs may produce one or more distinct gametes, or the contents may remain continuous, and the gametes be indicated by nuclei lying in an undifferentiated mass of cytoplasm. To multinucleate organs of the latter type the term **coenogametangium** is applied. Free-swimming gametes occur only in a few of the Archimycetes, and spermatozoids only in the genus *Monoblepharis*. In some of the higher fungi the entire antheridium is set free and may be carried by external agencies to the female organ; it is then termed a

spermatium, and the receptacle in which spermatia are borne a **spermogonium**.

A state of affairs in which the antheridium as a whole must grow, or be transferred, to the oogonium involves a risk that normal fusion will fail to occur, while at the same time the existence of coenogametangia, and of vegetative cells between which anastomoses readily take place offers considerable opportunities for "reduced" fertilisation. The replacement of normal sexual fusion by the union of two female or two vegetative nuclei, or of a female and a vegetative nucleus, is common among fungi, and the complete disappearance of even this reminiscence of a sexual process is still more frequent. It has been suggested that the variety of food material which fungi, as parasites or saprophytes, obtain from their substratum, may make the stimulus of fertilisation less important; it is also possible that among these plants competition is less severe than among holophyta or holozoa, and that, being already well adapted to a fairly constant environment, they would not benefit by the chances of variation involved in sexual reproduction. At any rate almost every group of fungi shows a progressive disappearance of normal sexuality.

The sexual fusion or its equivalent is followed in all investigated cases by a nuclear reduction or meiotic phase, so that, as in other plants and animals, the number of chromosomes, which was doubled in connection with the fertilisation stage, is subsequently halved in meiosis, and haploid and diploid phases follow one another.

Meiosis is associated with spore formation, and, in the lower fungi, appears ordinarily to take place on the germination of the zygote. In the normal life history of most of the higher fungi a period of vegetative development intervenes between the association of the nuclei in fertilisation or otherwise and chromosome reduction, so that there is a well-marked alternation of generations, in which the haploid gametophyte bears the sexual organs, and a diploid sporophyte gives rise to spores, which constitute the first stage of a new gametophyte. The sporophyte, in a considerable proportion of cases, is parasitic on the gametophytic mycelium. It is not uncommon to find several sporophytes arising from a single gametophyte, and, in many fungi, the gametophytic mycelium sends out branches which grow around and protect the

sexual organs and their products. When fertilisation or any equivalent process has wholly disappeared, a similar morphological alternation of sporophyte and gametophyte may be found, though without the corresponding cytological changes; but in some cases, as in the large collection of *Fungi imperfecti*, a sporophyte is no longer developed.

Spores and Spore Mother Cells. In the higher fungi the characteristic spores of the sporophyte, with the development of which meiosis is associated, may be produced either endogenously, as **ascospores**, in a mother cell of limited size termed an **ascus**, or exogenously, as **basidiospores**, on the exterior of a cell or row of cells known as a **basidium**. The asci or basidia are frequently arranged in parallel series, forming a fertile layer, or **hymenium**, sometimes of considerable extent; they arise from a **sub-hymenial** region immediately below the hymenium, and among them are interpolated vegetative cells, or **paraphyses**, which are perhaps concerned in their nutrition and which assist in spore dispersal by keeping the spore mother cells apart. The ascus and basidium and their products have long been recognised as essential features in classification.

In the lower fungi, the spores associated with the meiotic phase resemble those concerned in the accessory methods of multiplication.

Accessory Spores. The accessory or non-sexual methods of multiplication have no relation to a sexual process either normal or reduced, and therefore no significance in the alternation of generations; in other words, they are not homologous with the spores of the Bryophyta or Pteridophyta, but are devices for rapid increase comparable with the gemmae of *Marchantia* or the arrangements for vegetative propagation in the higher plants. The accessory spores may be borne on the sporophyte, as in the rusts and certain Autobasidiomycetes, or, as in the majority of Phycomycetes and Ascomycetes, on the gametophyte.

In many of the lower fungi, zoospores are developed in spherical or tubular zoosporangia; this is especially common in aquatic forms. In connection with the change from aquatic to subaerial conditions, the contents of the sporangium may come to be shed as walled non-motile spores, or the sporangium itself may be set free without division of its contents. Such a structure, borne ex-

ternally on its parent hypha, is termed a **conidium**, and is the characteristic unit of accessory multiplication among fungi. In the great majority of cases the conidium germinates by means of a germ tube, but, where the fungus has not completely abandoned an amphibious habit, the conidium, if it falls in a wet situation, may give rise to zoospores. Conidia are commonly developed, either singly or in groups, upon stalks known as **conidiophores**; these may be free; they may be gathered into a sheaf or **coremium**; they may constitute a hemispherical cushion termed a **sporodochium**; or they may be produced inside a special, flask-shaped receptacle, the **pycnidium**. They show an almost endless variety of form and arrangement.

A less common propagative cell is the **chlamydospore**; these are formed either singly or in chains in the course of the ordinary vegetative hyphae or on special branches; their development is associated with the loss of water, and, as their name implies, with the subsequent thickening of the wall.

It is not unusual for vegetative hyphae to divide into short segments which break apart, are disseminated, and give rise to new plants. To these structures the term **oidium** is applied.

Many conidia and other thin-walled spores possess the power of **budding**, giving rise, that is to say, to lateral outgrowths which are soon nipped off as new cells. This method of propagation is shown by the yeasts, in some of which it has wholly superseded the development of a mycelium. Ascospores are found to bud in the Exoascaceae, basidiospores in the Ustilaginales, and vegetative cells in species of *Mucor*.

Morphology of the Spore. The individual spore, whether it belongs to the principal or accessory fructification, is, when first formed, a single **hyaline**, that is, transparent, colourless cell; in the course of development it may divide and become a mass or row of cells, and, in the former case (fig. 178) is described as **muriform**; either its wall or its contents may become coloured, and its cytoplasm often develops large oil globules. The spore is usually enclosed in a double wall consisting of a delicate endospore and an epispore which may be smooth or sculptured. The sculptured epispore may show small projections and is said to be **verrucose**, or it may be reticulate, exhibiting more or less regular depressions between which anastomosing ridges are present. The spore may be borne on a specialised outgrowth, the **sterigma**.

Classification. The fungi are divided into three main classes according to the septation of their mycelium and the characters of their principal spores. The members of the fourth class, the *Fungi imperfecti*, multiply by conidia, and are probably, for the most part, incompletely known or degenerate members of the Ascomycetes, the mycelium and accessory fructifications of which they closely resemble. The lichens, though their dominant constituent is a fungus, differ from ordinary fungi in many of their characters, and have been so effectively dealt with in a recent volume by Miss A. Lorrain Smith[1] that it would be superfluous to include them here. *Collema pulposum*[2] and some other species, however, repay consideration in connection with the life histories of the higher Ascomycetes. The Myxomycetes are not fungi, and have probably a separate origin among the Protista; but, since they must be considered in any discussion of the ancestry of the fungi, a brief summary of their salient characters has been included. The same is true of the Plasmodiophoraceae.

There are numerous works on the classification, or classification and morphology of the fungi; among those which may usefully be consulted, given in the bibliography on p. 337, are Tulasne, 1861–5, which is of value for its admirable figures; de Bary, 1887, embodying the foundations of modern mycology; Swanton, 1909, a useful book for field work; W. G. Smith, 1908; Massee, 1911; Guilliermond, 1913; Gwynne-Vaughan, 1922; Rea, 1922; Ramsbottom, 1923; and the relevant portions of Rabenhorst's *Kryptogamen-Flora* and Engler and Prantl's *Pflanzenfamilien*. The figures of macroscopic fungi given in some of the above-named books may be used to supplement those in the present text, which have necessarily been reduced to a minimum.

The classes of fungi may be distinguished by the following characters:

FUNGI

vegetative mycelium usually aseptate	vegetative mycelium septate		
	characteristic spores endogenous, ascospores	characteristic spores exogenous, basidiospores	ascospores and basidiospores lacking
PHYCOMYCETES	ASCOMYCETES	BASIDIOMYCETES	*FUNGI IMPERFECTI*

[1] Smith, A. L., 1921.   [2] Bachmann, 1912.

They may be further subdivided as follows:

PHYCOMYCETES

mycelium absent
or rudimentary

mycelium well
developed

sexual reproduction by
oospores; accessory
spores often motile

sexual reproduction by
zygospores; accessory
spores non-motile

ARCHIMYCETES
1. Chytridiales
2. Ancylistales
3. Protomycetales

OOMYCETES
1. Monoblepharidales
2. Saprolegniales
3. Peronosporales

ZYGOMYCETES
1. Mucorales
2. Entomophthorales

ASCOMYCETES

ascocarp, if present,
either with no definite
opening, or shield-shaped,
or with asci irregularly
arranged

ascocarp wide open
when ripe, asci in
parallel series

ascocarp flask-shaped,
opening by an ostiole
when ripe; asci in
parallel series

PLECTOMYCETES
1. Plectascales
2. Erysiphales
3. Exoascales

DISCOMYCETES
1. Pezizales
2. Helvellales
3. Tuberales
4. Phacidiales
5. Hysteriales

PYRENOMYCETES
1. Hypocreales
2. Dothideales
3. Sphaeriales
4. Laboulbeniales

BASIDIOMYCETES

number of basidiospores
indefinite

number of basidiospores
definite, usually four

basidium septate

basidium continuous

HEMIBASIDIOMYCETES
1. Ustilaginales

PROTOBASIDIOMYCETES
1. Uredinales
2. Auriculariales
3. Tremellales

AUTOBASIDIOMYCETES
1. Hymenomycetales
2. Gasteromycetales

FORMS RESEMBLING FUNGI

MYXOMYCETES

The organisms which are placed in the Myxomycetes[1] are isolated and show signs of specialisation which cannot be reconciled with a position at the base of the fungi[2]. In early stages of development they appear as small, naked uninucleate amoebae, the **myxamoebae**, with a contractile vacuole, and other vacuoles into which solid material is taken; this mode of nutrition is adopted by the organism throughout its active life. Mitosis is followed by the division of the whole body, and repetitions of this process give rise to a large number of individuals. In the lower Myxomycetes, myxamoebae alone occur, but in more advanced types, the myxamoebae are converted into uniciliate pyriform zoospores; these retain some capacity for amoeboid movement, especially at the blunt posterior end, where pseudopodia are put out, and solid material is captured. The anterior end is drawn out to form a cilium, with which a blepharoplast is associated.

The zoospores increase in number by division of the nucleus and cytoplasm. Eventually, multiplication ceases, the zoospores reassume the myxamoeboid form and fuse in pairs[3] to give amoeboid zygotes. There is evidence that fusion can take place only between members of the two physiological types into which the zoospores are differentiated[4]. The zygotes come together in large numbers; in lower forms, a **pseudoplasmodium** of closely associated but distinct individuals results; in higher forms, the fusion of the cytoplasm of the zygotes gives origin to a **plasmodium**. Small plasmodia flow together to form larger ones, active growth accompanied by nuclear division occurs, and the plasmodium moves over or through the substratum, taking in and devouring solid material[5], including spores, zoospores and myxamoebae which have not fused. The plasmodium is a thin sheet of naked protoplasm, containing a network of rather dense strands in which streaming is well seen. As a rule, the area covered by an adult plasmodium does not exceed a few square inches; the plasmodium of *Fuligo varians* may cover more than a square yard.

[1] Lister and Lister, 1925.   [2] Pascher, 1918 ii.
[3] Jahn, 1911.   [4] Skupienski, 1918, 1920.   [5] Wilson and Cadman, 1926.

During the time that growth is active, plasmodia tend to move towards moisture, and to avoid strong light. Exposure to drought causes the formation of a dense mass of walled bodies; each of these contains about a dozen nuclei, and the whole mass constitutes a sclerotium. This is tolerant of adverse conditions, and may remain quiescent for some years. When water is supplied, the cellulose walls are absorbed, and a plasmodium reappears; the time required for the resumption of activity is roughly proportional to the duration of the period of desiccation[1].

Sooner or later the plasmodium changes its behaviour and moves towards a relatively dry position in good light. Protuberances form upon it in one or more places, and from these sporangia appear, singly or in groups. In the higher Myxomycetes, a mass of uninucleate spores develops within the sporangium, embedded in a system of threads or tubes, the **elaters**; these form the **capillitium**, in which hygroscopic movements bring the spores to the surface, whence the wind carries them away. As a rule, a single myxamoeba is produced when the spore germinates.

The nuclei of the spores, and of the myxamoebae, are haploid; the diploid condition is initiated when the zygotes are formed, and persists until spore formation, when a reducing division occurs[2].

PLASMODIOPHORACEAE

There are less than twenty species in the Plasmodiophoraceae[3], all endoparasitic in higher plants or in insects. In the vegetative stage, the organism is a naked mass of protoplasm, the myxamoeba; increase in size is accompanied by nuclear division, and ultimately the thallus breaks up into a number of walled spores.

The earliest known stage of *Sorosphaera Veronicae*[4] is a uninucleate myxamoeba lying in a meristematic cell of the stem of *Veronica*. Repeated nuclear division is followed by the cleavage of the body into a number of myxamoebae, which grow and, after nuclear division, give rise to new individuals. Meanwhile the host cell is stimulated to divide, myxamoebae are thereby passively distributed to the daughter cells, further divisions follow, and groups of infected and hypertrophied cells come into existence.

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[1] Jahn, 1919.   [2] Jahn, 1911.

[3] Woronin, 1878; Maire and Tison, 1909, 1911; Winge, 1913; Schwartz, 1914.

[4] Blomfield and Schwartz, 1910; Maire and Tison, 1911; Winge, 1913.

In a myxamoeba, all the nuclei divide at the same time, but division is not simultaneous in individuals associated in a host cell, even when they are so closely packed that they seem to be united into a common mass. Most of the stainable material of the nucleus of the vegetative phase is concentrated into a rounded body, which, when division is about to occur, is encircled by a ring of small granules. Each daughter nucleus receives half of the chromatin mass, and half of the ring.

As the myxamoebae become crowded in the host cells, oily material accumulates in their cytoplasm, the mass of chromatin dwindles, and stainable material is extruded from the nucleus, which is now difficult to demonstrate. After a time, nuclei again become apparent, now of ordinary type, with threads of chromatin. These nuclei divide, together with their associated cytoplasm; the products divide again, and the resulting uninucleate masses are converted into spores by the formation of a wall. As all the nuclei of a myxamoeba go through these changes at the same time, and as the spores are united by their walls, a group of spores results in the form of a hollow sphere, surrounded by a common membrane.

The germination of the spores has not been observed in *Sorosphaera*, but something is known of the process in other genera. The spore of *Spongospora subterranea* gives rise to a single uninucleate myxamoeba which moves by means of pseudopodia[1]; that of *Plasmodiophora Brassicae* liberates a naked, pyriform uniciliate zoospore[2]; somewhat similar bodies have been seen in water containing mature and empty spores of *Tetramyxa parasitica*[3].

There is evidence that part of the life cycle occurs outside the host; the vegetative body of *Cystospora batata*[4] emerges from the sweet potato, and may be collected on paper; it is probable that *Molliardia Triglochinis*[3] quits its host and completes development in the soil. The myxamoebae of *Spongospora subterranea* encyst under dry conditions[1], a possible adaptation to free life in the soil. Experiments show that host plants are invaded from soil into which spores of *Plasmodiophora Brassicae* have been introduced[5]. An investigation of the life led by these organisms in the soil is needed; it would throw light upon the difficult problem of control, and might lead to the discovery of a sexual act in the life history.

[1] Kunkel, 1915. [2] Chupp, 1917. [3] Maire and Tison, 1911.
[4] Elliott, 1916. [5] Woronin, 1878; Chupp, 1917.

During the vegetative phase, nutrition is largely a matter of the absorption of dissolved material; the myxamoebae of *Ligniera radicalis* are able to ingest algae[1], and it is possible that use is made of solid material when the organism lives in the soil. The activity of the parasite induces great changes in the cells of the host[2]; their nuclei become deformed, the cytoplasm degenerates, and finally the dead cell is occupied by masses of spores of the parasite. In general, cells containing chlorophyll are not attacked[3], and starch grains resist absorption for a long time. Invasion of the host may be effected through root hairs, through the surface of the root, or at growing points. *Cystospora batata* passes through cell walls within the host[4], and there is evidence that this capacity is also possessed[5] by *Plasmodiophora Brassicae*.

There is great variation in the effect on the host[6], and in the degree to which penetration occurs. Virulent parasites, such as *Plasmodiophora Brassicae*[7], induce much hypertrophy, and many abnormal divisions of the cells; a root may be attacked by many myxamoebae, and turnips and cabbages invaded by this species consequently show extraordinary deformations, to which the popular name of club root is applied. In normal soil, the invasion of potatoes by *Spongospora subterranea*[8] is confined to the outer tissues by the formation of cork beneath the seat of infection, but in wet soil, the deposition of cork is interfered with and the parasite may enter deeply. The species of *Ligniera*[9] are weak parasites; they attack moribund root hairs and cortical cells; these are not stimulated to divide, and, as hypertrophy is not caused, the root shows no deformation.

PHYSIOLOGY

SAPROPHYTISM, PARASITISM AND SYMBIOSIS

Since fungi never possess chlorophyll, they are dependent for their food upon some sort of relation with other organisms. As **saprophytes** they may utilise organic stores or waste products, or

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[1] Maire and Tison, 1911.

[2] Blomfield and Schwartz, 1910; Lutman, 1913; Kunkel, 1915, 1918; Chupp, 1917.   [3] Woronin, 1878; Lutman, 1913.

[4] Elliott, 1916.   [5] Lutman, 1913.

[6] Maire and Tison, 1909, 1911; Cunningham, 1912; Winge, 1913.

[7] Nawaschin, 1899; Favorsky, 1910.   [8] Osborn, 1911; Kunkel, 1915.

[9] Schwartz, 1914.

may break up dead tissues as a source of supply; as **parasites** they may prey upon living cells with consequences to the host that vary from trifling inconvenience to complete destruction; or as **symbionts** they may establish a relationship with another organism in which the advantages are not all on one side.

These physiological classes are connected by intermediate forms capable of changing their method of nutrition according to circumstances. A species which is strictly limited to one mode of existence is an **obligate** saprophyte, parasite or symbiont; a species which is usually saprophytic but capable of parasitic existence on occasion is described as a **hemi-saprophyte** or **facultative** parasite, and a form which is usually parasitic but sometimes saprophytic as a **hemi-parasite** or **facultative** saprophyte.

SAPROPHYTISM

According to our present knowledge the large majority of fungi are saprophytic; a considerable proportion of forms in each systematic class, and especially a very large number of the Basidiomycetes, obtain food in this way.

Aquatic Fungi. Submerged organic materials, as well as the remains of freshwater and marine organisms, furnish substrata for the growth of aquatic fungi; to most of these a plentiful supply of free oxygen is essential, so that they tend to develop in shallow water where little putrefaction is in progress. Humus and lime seem to have slight effect upon growth; mud, iron, and the metabolic products of sulphur bacteria are inimical. Although shade does not cause injury, aquatic fungi are most numerous in well-lit water, where the crowded population provides ample food[1].

The saprophytic forms are in general rather intolerant of competition; their development is hindered by the growth of algae, and by the accumulation of bacteria; lack of free oxygen is probably the critical factor involved. Most of the saprophytes belong to the Saprolegniaceae; species of *Saprolegnia* show a marked preference for animal substrata; *Achlya* and *Monoblepharis* occur on fallen twigs.

Certain species are relatively insensitive to poor aeration and to the presence of bacteria; *Gonapodya siliquaeformis* and *Macro-*

[1] Thaxter, 1895 i, ii, 1896 ii, iii; Petersen, 1903, 1910; Butler, 1907, 1911; Coker, 1923.

chytrium botrydioides live under dense masses of bacteria in foul water where oxygen is scarce; they are probably facultative anaerobes[1].

Running water harbours a few characteristic forms. Water which is not acid to litmus, and contains simple, organic compounds of nitrogen may show an extensive development of *Leptomitus lacteus*; water of similar reaction, but with little combined nitrogen and some carbohydrates, may contain *Sphaerotilus natans*; with more carbohydrate, species of *Mucor* develop, and, in the presence of free nitric acid, heavy growths of *Penicillium fluitans* are observed[2].

Several of the aquatic saprophytes are themselves attacked by fungal parasites, and parasitic fungi are also found on members of the Conjugatae and other green algae, on brown and red marine forms, and on water animals[3].

On Wood. Ascomycetes and Basidiomycetes are important agents in the destruction of wood[4]; their hyphae absorb the contents of the living cells of the xylem and medullary rays, and enter the fibres, vessels and tracheids, either passing through the pits or penetrating the walls. The walls become delignified and give cellulose reactions, and the middle lamella is dissolved. The action of the enzyme responsible for these changes spreads in a plane parallel to the surface of the wall, either from the pits, which become enlarged, or from the delicate passages left by the protoplasmic connections which traversed the walls of the wood elements when these were young. The whole mass of wood loses weight and may reach the powdery condition known as touchwood. In this way considerable damage is done to timbers by the fungi of dry rot[5], *Merulius lacrymans* and *Poria vaporaria*, to paving blocks by *Lentinus lepideus*[6], and to a variety of other structures. On the other hand important advantages ensue from the restoration to the soil of the material of fallen tree trunks, twigs and branches. The action of the higher fungi in this connection is especially important, as the only other agents of destruction of

[1] von Minden, 1916.   [2] Tiegs, 1919.
[3] Fischer, A., 1882; Church, 1893; Juel, 1901; von Deckenbach, 1903; Petersen, 1905; Cotton, 1908; Chatton and Roubaud, 1909; Apstein, 1911; Sommerstorff, 1911; Brierley, 1913; Moral, 1913; Sutherland, 1914–15; Dunkerly, 1914; Ferdinandsen and Winge, 1920; Mirande, 1920; Maire and Chemin, 1922; Arnaudow, 1923.
[4] Ward, 1898; von Schrenk, 1902.   [5] Czapek, 1899.
[6] Buller, 1905, 1909 i.

lignified tissues appear to be molluscs, crustacea which bore into wood, and the larvae of beetles.

In Soil[1]. Fungi are largely confined to the top six inches of soil, where the forms most frequently found in temperate climates are species of *Penicillium* and *Mucor*; *Aspergillus* and such Hyphomycetales as *Fusarium* and *Cladosporium* are also common. Several fungi, and especially species of *Penicillium* and *Aspergillus*, and some of the Hymenomycetales actively decompose cellulose[2], while others, such as the Mucorales, have little effect in this direction. In the presence of ample supplies of carbohydrate, soil fungi utilise amino-acids as sources of nitrogen; when the available carbohydrates are insufficient, they obtain both energy and nitrogen from the protein compounds in the soil, but the process is an extravagant one and surplus ammonia is set free[3]. Both ammonia and nitrates can be assimilated, but, unless in the case of species of *Phoma*[4], the power to fix gaseous nitrogen does not appear to exist.

In addition to the micro-fungi, some Discomycetes and a large number of Autobasidiomycetes develop on soil; among these the members of the Tuberales, Elaphomycetaceae, Terfeziaceae and Hymenogastraceae are completely subterranean, or **hypogeal**, in their development. They produce closed fructifications protected by a stout wall; as the spores approach maturity the fruit emits a strong scent, which attracts animals, especially rodents. The fructification is eaten, the spores pass uninjured through the alimentary canal, and are thus distributed. The truffles, belonging to the genus *Tuber*, are the best known of such forms.

Species with subaerial sporophores are to be found both under trees and in open ground; their activities are well exemplified by the **fairy rings**[5] of dark green grass often seen in poor pastures. The ring is caused by the growth of a fungus, usually one of the Autobasidiomycetes, though rings due to the agency of the Ascomycetes, *Tuber* and *Morchella*, have also been reported; both the structure of the ring and the distribution of the mycelium vary in detail according to the fungus concerned. The mycelium spreads from the centre of infection, dying off as the food materials in the

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[1] Dale, 1912; Hall, 1920.   [2] McBeth and Scales, 1913; Scales, 1915.
[3] Waksman, 1918.   [4] Duggar and Davis, 1916.
[5] Hutton, 1790; Gilbert, 1875; Lawes, Gilbert and Warrington, 1883; Molliard, 1910; Bayliss, 1911; Shantz and Piemeisel, 1917; Buller, 1922 ii.

soil are exhausted. At the advancing margin ammonium com-
pounds are set free, and converted by bacteria into nitrates, stimu-
lating the development of a ring of dense vegetation. Just behind
this, where the growth of the fungus is especially energetic, the
resistance of the felted mycelium to the passage of water may cause
local drought and the formation of a brown ring of dead vegetation.
Still nearer the middle of the ring the soil contains degenerating
mycelium and the products of its decomposition favour the de-
velopment of a circle of strongly growing grass and other plants.
The soil in the central region has already passed through these
changes and the vegetation which it bears does not differ essen-
tially from that in the remainder of the field. In wet seasons and
where the development of the mycelium is insufficient to cause
local drought, the activity of the fungus is represented by a single
ring of stimulated vegetation. The rings are often distinct enough
to show well in photographs from the air.

Coprophilous Fungi. Fungi feeding on organic remains in the
soil often benefit by the presence of natural manures, and incident-
ally often help to break up these substances, rendering them
available for the use of green plants.

From such fungi it is no great transition to the extensive **copro-
philous** flora, characterised by its habitat on the dung of animals[1]
and especially of herbivorous species. In addition to the rich
nitrogenous food which these fungi obtain, the presence of cellu-
lose in the straw and other debris of the dung is an important
factor in their nutrition. Specimens often occur in close associa-
tion with such material, and many coprophilous species fail to fruit
in artificial culture on dung agar unless cellulose in the form of
scraps of cotton wool, filter paper or grass is incorporated in the sub-
stratum. In nature Zygomycetes, Ascomycetes and Basidiomycetes
succeed one another in fairly regular order, and show similar
adaptations to their habitat. In many of the Ascobolaceae and
Sordariaceae among Ascomycetes the spores are surrounded by
mucilage and together form a projectile which, owing to its weight,
can be shot to a much greater distance than a single spore. The
sudden ejection of the mass seems to depend on the rapid forma-
tion of sugars of high osmotic value and the consequent absorption
of water and bursting of the ascus wall. After ejection the mass

[1] Massee and Salmon, 1901.

dries up and remains firmly attached to the grass or leaves on which it has fallen. Similarly the spores in the sporangium of the mucoraceous genus *Pilobolus* are associated with gelatinous material, and, when the wall bursts, the upper part of the sporangium and the contained spores are shot off as a single mass and adhere to the body against which they strike. The grass surrounding the dung thus receives an ample supply of spores; later, if it is eaten by some herbivorous animal, these pass through the alimentary canal and germinate while still in the intestine or after ejection with the dung. In some cases the wall of the spore has become so effectively adapted to resist injury in its passage through the animal that it is incapable of stretching or cracking as a preliminary to germination except after digestion or some other special treatment. Warming for some hours in an alkaline solution, exposure for a few minutes to temperatures of 50° to 70° C., and mechanical rupture by rubbing between coverslips are among the methods which have proved effective. In many cases the presence of bacteria is necessary both in relation to germination and to subsequent development[1]; and this, since the number of bacteria in the dung changes with its age, may be a factor in the succession of species of fungi.

Another factor of some importance in the development of coprophilous as well as of other[2] fungi is the action of direct sunlight. Cultures which remain sterile in the dark can often be induced to fruit by placing them in a sunny window; possibly the light and warmth thus provided may facilitate the chemical changes essential to development. Many coprophilous species, moreover, show positively phototropic reactions, the sporangiophores of *Pilobolus*, the perithecium necks of *Sordaria*, and the individual asci of some of the *Ascoboli* being regularly directed towards the light. The ejection of the spores towards an open space is thus ensured.

A large proportion of the coprophilous Ascomycetes have recently been shown to possess conidial forms; the conidia germinate readily, and serve to reproduce the fungus without the digestion or its equivalent required in the case of ascospores. In nature the conidia doubtless germinate on grass or refuse, and the ascospores in many cases only on ejection with the dung.

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[1] Molliard, 1903; Baden, 1915; Sartory, 1918.
[2] Cf. p. 37.

Fungi on fatty substrata. Most fungi are able to utilise fats and oils; such substances are a common form of food reserve in spores, in the mycelium, and especially in sclerotia, where the proportion of fat may reach as much as 35 per cent.; in several cases the fat-splitting enzyme, lipase, has been isolated.

It is therefore not surprising that many fungi grow readily on fatty substrata[1], some on animals or their remains, some on other fungi, some on oil cake, the oil content of which they have been known to reduce from 10 per cent. to between 1 and 2 per cent. *Eurotium* and *Penicillium* may be found on the layer of oil placed over bottled fruits to prevent decomposition, and, together with other genera, are concerned in the "ripening" of cheese; the related *Monascus heterosporus* does considerable damage in parts of Australia and New Zealand if allowed to get a footing on stored tallow.

Fungi producing fermentation. A number of fungi obtain nutriment from solutions of carbohydrates, and the yeasts also obtain energy by breaking up these substances without the intervention of free oxygen. When such anaerobic respiration is incomplete, ethyl alcohol, carbon dioxide, and small quantities of other substances are formed. Many organisms are capable of this process as an emergency reaction, but in yeast it has become the normal routine, and may be regarded as the adaptation of a group of simple forms to a mode of life with a minimum of competition.

The reaction depends on the presence of the enzyme zymase, and is known as alcoholic fermentation. In its least complex form it may be represented by the equation:

$$C_6H_{12}O_6 = 2C_2H_6O + 2CO_2.$$

Zymase is secreted by the cells during their period of fermentive activity, but is not present in resting cells, being soon decomposed when the reaction comes to an end. It is made up of two co-enzymes; one is a soluble phosphate which enters into temporary combination with a part of the carbohydrate, but is ineffective in the absence of a second factor of unknown constitution. The unknown co-enzyme is dialysable and is not destroyed by boiling; it may be separated from yeast juice by filtration under pressure, both filtrate and residue being inactive alone.

[1] Biffen, 1899.

Only certain monosaccharides with the formula $C_6H_{12}O_6$, such as glucose and fructose, are capable of undergoing alcoholic fermentation; polysaccharides, such as cane sugar, lactose and maltose, must be hydrolysed with the production of appropriate monosaccharides before fermentation can take place. Hydrolysis depends, in nature, on the excretion into the liquid of the enzyme invertase by the fungal cell.

A number of yeasts are utilised economically, both in baking, where their value depends on the formation of carbon dioxide, causing the bread to "rise," and in brewing and other processes concerned with the production of alcohol. The characteristic yeast of wine, which ferments grape sugar, is found in abundance at vintage time on the grapes and their stalks, and the cider yeast is found on apples. The yeast of beer, on the other hand, which acts on the sugar formed in germinating barley, is not known in the wild state.

In the production of numerous alcoholic beverages yeast acts symbiotically with one or more bacteria or fungi[1]; this is the case in the "ginger beer plant"[2] which, added to commercial ginger, sugar and water, causes the formation of ginger beer. The "plant" has the appearance of lumps of soaked tapioca or sago; its essential constituents are the yeast, *Saccharomyces piriformis*[3], and the bacterium, *B. vermiforme*. The bacterium is able to utilise the products of metabolism of the yeast; the yeast benefits by the removal of these substances, the accumulation of which would inhibit its development; the relation of the two organisms is thus a symbiosis in which each gains by its association with the other.

Zymase is also secreted by several filamentous fungi; *Mucor racemosus* and certain other species[4], when cultivated in sugar solution, form ovoid cells which multiply by budding and cause active fermentation. This is especially the case in the presence of organic acids, or when aeration is insufficient.

Soot Fungi. The soot fungi, like the wild yeasts, are epiphytic saprophytes; they occur on leaves frequented by green fly and obtain their food from the "honey dew" excreted by these insects. Their dark-coloured mycelium forms a sooty coating on the leaves of the host, but is not thick enough to injure them by excluding light.

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[1] Klöcker and Schiönning, 1895, 1896. [2] Ward, 1892.
[3] Guilliermond, 1920 ii. [4] Nadson and Phillipov, 1925.

PARASITISM

Facultative Parasites. Fungi which are capable of passing through their whole development as saprophytes are also sometimes found on living plants. They possess the power of disintegrating the tissues in advance, so that they are not parasitic in any strict sense, but first kill the cells of their host and then live saprophytically on the dead remains[1]. This is well seen in *Botrytis cinerea*; if the spores are placed in a drop of nutrient fluid on a leaf of the broad bean they show the first signs of a germ tube in two or three hours; the outer walls of the developing tube soon become modified to form a mucilaginous sheath by means of which the fungus adheres to the substratum. If a drop of distilled water instead of nutritive solution is used, substances may be found to diffuse into it from the host. According to the character of the host and of the fungal spores, such substances may stimulate germination, may produce no appreciable effect, or may even inhibit development. In the case of *Botrytis* on the broad bean some nutritive supply, whether due to exosmosis or artificially provided, is essential.

After growing for a while along the surface of the leaf, the germ tube turns down, and its tip, filled with dense protoplasm, is pressed against the cuticle of the host, where it may become spread out to form a simple **appressorium**; as growth continues the tube is held in place by its mucilaginous coat, and the cuticle is ruptured by the pressure of its tip. The fungus now either penetrates directly into an epidermal cell or grows more or less horizontally in the subcuticular layers; in either case these layers become swollen and appear to stretch the cuticle so that its penetration by other germ tubes is easier. As the hyphae travel through the epidermis the palisade parenchyma becomes affected, the nuclei begin to disintegrate, the chloroplasts swell, and most of the starch disappears. In the bean a dark coloration, which is one of the signs of death, spreads through the mesophyll in advance of the hyphae. The latter have been shown to secrete an enzyme which both disintegrates the walls of the host cells and causes the death of the protoplasts; it is unable to affect the cuticle, the penetration of which is always mechanical.

[1] Brown, W., 1915; Blackman and Welsford, 1916; Brown, W., 1916–23; Dey, 1919; Boyle, 1921.

Penetration of the cuticle, however, is by no means a necessary preliminary to parasitism, whether obligate or facultative, for the hyphae of many fungi enter the host through the stomata, while in others, the so-called **wound-parasites**, infection only takes place where the internal tissues have been exposed or damaged.

Once established within the host organ, the fungus may enter or send branches into the cells, or it may develop wholly in the intercellular spaces, killing those cells with which it comes in contact and benefiting from the food materials that diffuse out from the dead protoplast; such forms may be described as saprophytic in the same sense as *Botrytis*.

Fungi of which the attack is directed mainly to the elements of the wood flourish equally well on living and dead tissues; the harm which they do to their host largely depends on the fact that they cut off the water supply from regions above the infected area. This is the case with *Nectria cinnabarina*[1], and the fact that in this species ascocarps are produced on dead tissue emphasises its hemi-saprophytic character, and demonstrates that the survival of the host is not essential to the attacking fungus; there is evidence that the appearance of ascocarps is here associated with a change in the carbon nitrogen ratio.

Obligate Parasites. In the case of obligate parasitism[2], on the other hand, the death of the host involves the death of the fungus, and it is to the advantage of the parasite that death should be postponed, at least until the latter has made provision for reproduction.

The relations of the parasite to its host are exceedingly varied. Among **endophytic** forms, which invade the tissues of the host, unicellular parasites go through their whole development in a single cell, while the higher fungi live mainly in the intercellular spaces or under the cuticle, and send short branches into the cells. These branches may become specialised as **haustoria** of limited growth and definite form.

In other cases the development of the parasite is external and may be described as **ectophytic**. This occurs in the mildews, or Erysiphaceae, which obtain their supplies by sending haustoria into the epidermal cells of the host, and in the Laboulbeniales, where food is absorbed through the unbroken membranes of the infected insect, and the parasite seems to cause a minimum of inconvenience.

[1] Line, 1922.   [2] Brooks, 1923, 1924.

The adaptation of the parasite to its method of life is shown at a very early stage in development. Thus the zoosporangia of *Cystopus candidus* form spores most readily at low temperatures, their minimum is near zero[1], their maximum about 25° C. and their most favourable temperature under ordinary circumstances 10° C. The spread of the fungus by zoospores depends on the presence of fluid water; a fall of temperature leads to the deposition of dew, and thus at the same time provides the condition for the activity of the zoospores and serves as a stimulus to their development. The aecidiospores and uredospores of rusts[2], on the other hand, which give rise to a germ tube directly, grow best at a temperature of 14° C. or more, varying among themselves according to the time of year at which the spores germinate in nature. The high temperatures appropriate to the germination of coprophilous spores may also be recalled in this connection.

The susceptibility of the host, or its resistance to the attacks of the parasite, varies in many cases with the environment; thus umbellifers growing in damp, shady situations are more liable to infection by *Protomyces*[3] than those in exposed habitats, and the same is true of the hosts of the Chytridiales[4], though here the fact that the zoospores require water in which to swim may be more important than the lessened resistance of the host. Again, the wild sloe is able to combat the attacks of silver leaf, to which its presumed descendant the Victoria plum, falls a ready victim; it is possible that, in such a case, the factor for resistance may have been bred out.

The relation between the parasite and its host may be strictly localised, as in the case of the Laboulbeniales and of many unicellular parasites, or the fungus may spread far beyond the point of infection and may keep pace with the growth of new tissues. Perennial mycelia are not uncommon among Exoascaceae, rusts, and other forms which infect trees, and in some cases the mycelium is found year after year in the tissues of a geophilous host, dying down when the latter prepares for winter, and growing again with the renewal of its growth.

The parasite may modify the host tissues by its invasion, chiefly in the direction of abnormal growth or **hypertrophy**. The

[1] Melhus, 1911.
[2] Robinson, 1914; Doran, 1919.
[3] von Büren, 1915.
[4] Tobler, 1913.

simplest instance of an effect of this kind is the enlargement of a single cell such as is found in the infection of filamentous fungi by *Olpidiopsis*, or of the dandelion and other angiosperms by *Synchytrium*; in the latter case the cells surrounding the seat of infection are also enlarged and stimulated to abnormal division.

It is not uncommon for fresh cell formation to take place; this may be limited to the neighbourhood of the infected spot so that the host organ becomes locally deformed; thus peach leaf curl and many similar abnormalities are formed by *Exoascus* and its allies, and irregular, rose-coloured blisters appear on the leaves of Ericaceae when attacked by *Exobasidium*. More elaborate deformations are produced by some of the Ustilaginales and, in the case of witches' brooms, by the rusts and Exoascaceae.

A witch's broom is a bunch of modified twigs, due usually to insects, but sometimes to fungi. In the latter case it is the product of a lateral bud, which, stimulated by the presence of the fungus, or by the food which the fungus deflects from its proper course, grows out to form an abnormally dense bush of twigs; the production of flowers is inhibited, the leaves appear earlier than those of healthy branches, and, in the case of evergreen conifers, fall off at the end of each season. The affected shoot, in spite of its contained parasite, appears at first to flourish, though to the detriment of the rest of the tree; it may be suggested that something approaching symbiosis has been locally established, but in this case the fungus is clearly the gainer.

SYMBIOSIS

The physiological conditions under which the thallus of a lichen is built up are somewhat similar; the algal cells appear healthy; they are capable of vegetative multiplication, and sporulation occurs in the algal constituent of *Evernia prunastri*[1]. The fungus alone is concerned in the development of the fructification, a clear indication that it plays the dominant part in the association.

The term **mycorrhiza** is applied to the structures formed by the association between the mycelium of a fungus and the roots or other organs of one of the higher plants[2]. The mycelium may

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[1] Paulson, 1921.
[2] Reissek, 1847; Frank, 1885, 1891; Weiss, 1904.

be **endotrophic**, occurring within and between the cells of the host, and having little connection with a mycelium in the soil; or it may be **ectotrophic**, with a strong development on the surface of the root, and a limited distribution within the tissues. There is little evidence that nitrogen[1] is brought into combination by the fungus and utilised by the green plant; it may be that the activity of the fungus raises the concentration of the dissolved carbohydrate[2] in the cell sap, and that this change provokes reaction in the host, stimulating active growth which leads to the consumption of excessive carbohydrate in respiration, or induces the formation of storage organs where superfluous material may be immobilised as starch. However this may be, it seems clear that the fungus takes the first step in the formation of the association, acts for a time as a parasite, and eventually succumbs to the higher plant. The latter may be little affected; it may, as in orchids and Ericaceae, depend on the co-operation of the fungus for the successful negotiation of a crisis in the life history; or, as in *Gastrodia* and other saprophytes, it may be unable to survive in the absence of the fungus.

Endotrophic Mycorrhiza. Fungal hyphae occur casually in the cortex of the roots of many perennial flowering plants and vascular cryptogams. In these cases, the fungus enters from the soil and lives as a parasite in the outer layers of the root; in deeper-lying and presumably better nourished cells its progress is arrested. Tangled, dichotomously branched tufts of hyphae are formed in this region; they are digested by the host and leave dead residues of rounded form. Penetration may extend to the cells lying just outside the endodermis, but in healthy roots never goes deeper than this. The fungus does not form spores within the host, and fails to establish itself permanently as a parasite; it is possible that the vascular plant benefits to some extent from the digestion of the hyphae. However, there is no constant association; many roots contain no fungus, and evidence is lacking that infected plants do better than non-infected ones, or that the fungus gains in any way[3].

A similar condition obtains in the gametophyte of the liverworts[4], where an endophytic mycelium may be found, usually in

[1] Ward, 1888 ii; Ternetz, 1907; Burgeff, 1909; Goddard, 1913; Rayner, 1915.
[2] McLennan, 1926.   [3] Gallaud, 1905.
[4] Cavers, 1903–4; Ridler, 1922–3; Magrou, 1925.

the ventral cells of the midrib; the fungus does not enter cells rich in starch, and the sporophyte remains uninfected.

Rounded wefts of hyphae occur in the cortical cells of the young roots of orchids[1]; fructifications are not produced within the healthy host plant, but the fungus may be isolated and grown in culture; it belongs to the form genus *Rhizoctonia*[2], some members of which are conidial stages of *Hypochnus*. The distribution of the fungus within the orchid varies with the characters of the latter: *Cattleya* is rootless for a portion of the year, and at that time does not contain a fungus; *Vanda* has perennial, permanently infected roots; infection is irregular in *Listera*, a genus rich in chlorophyll, and strong in *Corallorhiza*, in which chlorophyll is feebly developed; *Neottia*, a brown saprophyte, is always heavily infected. The rhizomes of *Gastrodia elata*[3] are attacked by *Armillaria mellea*, and the creeping stems of *Goodyera repens*[4] are occasionally entered by the fungus abundant in the roots.

The seeds of the Orchidaceae are small, and contain an undifferentiated embryo when they are set free from the capsule. Such seeds, extracted under aseptic conditions from the fruit, and sown on sterilised media, swell somewhat and turn green, but do not germinate; when however the seeds are sown in company with the fungus from the roots of the plant, seedlings are obtained[2]. A hypha grows into the suspensor end of the seed and invades the cells; in each cell a ball of hyphae is formed before the next is entered. While this is going on, divisions of the cells at the opposite end of the seed lead to the differentiation of the stem and root; general swelling occurs, and the seed is transformed into a green protocorm. The base of the protocorm is occupied by cells containing balls of hyphae. At the apex, the embryo is formed from a meristem which is not invaded by the fungus; the intermediate region consists of cells which have a marked capacity for digesting hyphae, and so prevent general infection. The young, endogenous root of the seedling burrows its way through the protocorm; it emerges uninfected, penetrates the soil, and is there attacked by the endophyte[5].

The seeds of some orchids will grow although no fungus is

[1] Magnus, W., 1900; Bernard, 1909–11; Ramsbottom, 1922.
[2] Bernard, 1909; Ramsbottom, 1922.   [3] Kusano, 1911.
[4] Costantin and Dufour, 1920.   [5] Ramsbottom, 1922.

present. Those of *Bletilla hyacinthina*[1], sown on sterile media, give slender seedlings very different from the protocorms developed in the presence of *Rhizoctonia*; the seeds of *Cattleya*[2] and *Laelia*[2] germinate in moderately concentrated solutions of carbohydrates; growth is slower than when the fungus is available, but protocorms are formed, and good seedlings obtained. *Rhizoctonia* is stated[1] to raise the concentration of nutrient solutions in which it grows; maybe, within the seed, the concentration of the cell sap is increased, and a stimulus given to germination similar to that afforded when seeds of *Cattleya* are placed in a solution of a carbohydrate. But, although it is possible, by suitable technique, to bring about the germination of the seeds of some orchids in the absence of the fungus, such orchids are normally dependent on the fungus at this stage of their life history.

The Ericaceae resemble the Orchidaceae in the frequent occurrence of hyphae in their roots, and in the possession of small seeds. *Calluna vulgaris*[3] lives in association with a species of *Phoma*. The mycelium occurs not only in the roots and other parts free from chlorophyll, but also in the stems, leaves, flowers and fruits; the demonstration of the fungus in these parts demands careful manipulation. When the seed germinates, hyphae present in the seed coat infect the seedling and normal development takes place. Seeds deprived of their fungus by sterilisation of the testa, and sown on sterilised media, give rise to seedlings with no roots; such weak seedlings grow vigorously when brought into relation with the fungus after it has been isolated and grown in culture. Strong seedlings are obtained by sowing seeds and inoculating them with the fungus. The relation here is one of controlled parasitism, for, if a weak seedling is inoculated from a strong culture of *Phoma*, it is killed by the fungus[4].

Ovarial infection occurs in other members of the Ericaceae, and the mycelium may possibly permeate the whole plant, as it does in *Calluna*. The closely related Pyrolaceae[5] include some green plants and some saprophytes; all are associated with fungi, the saprophytes markedly so. Correlated with the tendency in the family to adopt the mycorrhizal habit, there is a tendency to

[1] Bernard, 1909. [2] Bernard, 1909; Knudson, 1922.
[3] Ternetz, 1907; Rayner, 1915–21; Dufrenoy, 1917; Christoph, 1921.
[4] Rayner, 1915. [5] Oliver, 1890; Henderson, 1919.

increase the number of seeds and to reduce the size and complexity of the individual seed. A similar state of affairs is found in the Burmanniaceae and Gentianaceae[1].

In all these cases, the dependence of the higher plant on the fungus is obvious; the successful germination of the seed cannot take place unless the fungus is present; in the saprophytic forms, and in forms which contain some chlorophyll, the production of flowers is stimulated by the presence of the endophyte.

The dependence of the seed plant on the fungus during vegetative development is shown in *Gastrodia elata*[2], a non-chlorophyllous orchid found in oak woods in Japan. The vegetative part of the plant consists of a tuberous rhizome; this produces long branches, at the ends of which new tubers are formed; in autumn the latter become separated by the death of their stalks and of the parent body. In the outer cells of the tuber, the mycelium of *Armillaria mellea* acts as a parasite, but, further in, the tables are turned, and the invading filaments are destroyed. Association with the fungus is essential to the well-being of *Gastrodia*; when no union takes place, the orchid fails to flower and the newly formed tubers fall off in size; when isolation from the fungus is maintained for several seasons, the tubers are so much weakened that they are unable to give rise to a fresh crop, and the plant dies. *Gastrodia* is evidently parasitic on the fungus, and depends on it for supplies of nutrient material; *Armillaria* appears to benefit only occasionally when it succeeds in destroying the tubers it has entered.

The genus *Lolium*[3] presents a condition distinct from the cases already described. The roots contain an endophytic fungus; in the outer cells it is a weak parasite; in deeper cells, the invader is digested with the liberation of fatty material. Hyphae also occur in the grain, between the aleurone layer and the outer covering; at about the time of fertilisation, hyphae may be seen in the embryo sac; they grow at the expense of the nucellus and the carpel wall. If fertilisation is prevented, a sclerotium-like body is formed within the ovule; when fertilisation occurs, the endosperm digests some of the hyphae, to the advantage of the developing embryo. This is invaded, the hyphae taking up a position in the apex of the young shoot; they move up with the growth of the stem, accu-

[1] Stahl, 1900.　　　　　　　　　　　　[2] Kusano, 1911.
[3] McLennan, 1920, 1926.

mulate at the base of the young carpels, and increase in quantity when the ovules are formed. The fungus has not been isolated from *Lolium*, and it has not been shown that the hyphae in the roots belong to the same species as those in the fruit. It seems probable, indeed, that two fungi are present, one a weak parasite in the roots, ultimately digested by the grass, the other a degenerate seed parasite, persisting in a weakened condition, and so enslaved that it does little more than assist in the nutrition of the embryo.

Endotrophic mycorrhiza is well developed in the prothallus of *Lycopodium*, in the leafy plant of species of *Lycopodium* and *Sela-ginella*, in the roots of *Cyathea* and members of the Marattiaceae, and in the prothallus and sporophyte of the Psilotaceae and Ophio-glossaceae. The presence of a fungus appears to have little effect on the sporophyte, but there is evidence that the germination of spores in the Ophioglossaceae and Lycopodiaceae depends on the fungus; in the presence of a mycelium, the prothalli may be sub-terranean and devoid of chlorophyll; protocorms and tuberous structures are formed[1].

Nearly all wild perennial plants have fungi associated with their roots, whereas in annuals, this is not the case; when swollen perennating organs are formed, they remain free from the fungus, which is confined to the absorbing roots. The connection between the presence of a fungus and the development of tubers or rhi-zomes, is indicated by a comparative study of certain closely re-lated annual and perennial species[2]. Thus, *Orobus coccineus* is an annual, with a richly branched subaerial stem; tubers are not formed, and though young roots may be attacked by a fungus, the invader is soon completely digested. *Orobus tuberosus* is a perennial; the flowering branches are relatively simple and spring from a branching underground system of stolons, on which tubers freely develop; the roots always contain a fungus, even during the winter. If, however, seeds of *Orobus tuberosus* are sown in sterilised soil, after sterilisation of the testa, they give rise to seedlings very like those of *O. coccineus*; the plants branch freely above the soil, and tubers are not formed. The genus *Mercurialis* offers a suggestive parallel: *Mercurialis annua* is a much-branched annual which con-tracts no lasting union with a fungus; *Mercurialis perennis* branches little above ground, perennates by means of a rhizome, and har-

[1] Stahl, 1900; Lang, 1902; West, 1917.   [2] Bernard, 1911 ii; Magrou, 1921.

bours a fungus in its roots. Similar relations are found in wild species of *Solanum*, but efforts to ascertain the cause of tuberisation in the potato suggest that a stimulus to the formation of tubers, comparable with that normally exerted by the fungus, is afforded by cultivation in richly manured soil. *Solanum Maglia*, a possible ancestor of the potato, forms tubers, and contains an endophyte in its roots. It may be surmised that, in cases such as these, the production of an organ of perennation, apparently proof against the fungus, protects the plant from attack during periods of inaction, when the cells are unable to digest an invader.

A condition recalling that found in endotrophic mycorrhiza is encountered in some insects belonging to the Coccideae[1]. The bodies of *Lecanium hemisphericum* and related species contain large numbers of yeasts; the eggs are infected during development, so that the fungus is passed on from generation to generation. The insects do not seem to suffer injury; they feed on plant juices, and it may be that the yeasts afford assistance in the elimination of the large amounts of carbohydrate material taken in by the insects.

Ectotrophic Mycorrhiza. Many woody plants possess an ectotrophic mycorrhiza[2], appearing as a dense felt of hyphae over the apical parts of the infected roots; the development of root hairs is impeded, and short coralloid branches are formed. The fungus makes its way between the outer cells of the root, and also penetrates some of the cells, where digestion of the hyphae apparently occurs. Infection of the young roots may take place at any period in the life of the green plant, but all young roots are not attacked; mycorrhiza is developed most strongly on roots which spread horizontally in layers of decaying leaves, or in masses of moss, lying beneath the canopy of the branches; it is rare or absent when the soil lacks humus; the roots then bear hairs, and function normally.

The relation between an ectotrophic fungus and its host, at least when the latter is green, appears to be more casual than is the case with endotrophic forms. The association probably arises as an attempt at parasitism on the part of the fungus; indeed, when external conditions are unfavourable to the fungus, the latter may become so strongly parasitic as seriously to damage the root.

[1] Conte and Faucheron, 1907.
[2] Frank, 1885; McDougall, 1914; Melin, 1921; Peyronel, 1921; Paulson, 1924.

Probably the fungus gets more out of the association than do the fungi of endotrophic mycorrhiza; perhaps there is a connection between the constant occurrence of certain agarics beneath certain trees and the mycorrhizal habit, the fungus being unable to fruit unless it is associated with an appropriate root. Thus, *Amanita muscaria* is commonly found under birch, *Lactarius deliciosus*, *Russula fragilis* and *Boletus badius* are characteristic of pine woods, and *Boletus versipellis* and *B. scaber* occur under deciduous trees. The brick red colour of the mycelium of *Cortinarius rubipes*[1] has made it possible to trace a connection between the fructifications of this fungus and young roots of oak. On the other hand, birches and hornbeams appear specially liable to the attacks of *Melanconis stilbostoma* and *Pseudovalsa lanciformis*[2] during times of drought, when the mycorrhiza has been killed off; this susceptibility may be due to the breaking up of the association, though it may be merely a result of general weakening caused by dry conditions.

It seems likely that the fungi of ectotrophic mycorrhiza take up material from the substratum and pass some of it on to the associated plant[3]; there is no evidence that these fungi influence germination.

SPECIALISATION

Fungi vary in the extent to which they are adapted or restricted to a particular habitat; in some species the range is wide, as in the case of *Eurotium herbariorum* or *Penicillium glaucum* which may occur, under suitable conditions of temperature and moisture, on almost any plant remains, on plant products, such as bread or jam, or on substances of animal origin, such as cheese or leather.

Similarly *Synchytrium aureum* infects all sorts of dicotyledons and *Phyllactinia Corylea* occurs on the leaves of many trees.

In other cases the range is narrowed; many species of *Hydnum* are found only in fir woods, *Pyronema confluens* and several other fungi occur in nature only on burnt ground, *Onygena equina* is restricted to the derelict horns and hooves of animals, and several species are found only on dung. Other fungi are limited, either as parasites or saprophytes, to the members of a particular family, a particular genus, or even a particular species.

[1] Kauffman, 1906.   [2] Paulson, 1924.   [3] Rexhausen, 1920.

Biologic Species. Such specialisation may be associated with definite morphological characters, or it may be purely physiological, so that a number of forms, identical in their minute structure, differ in their capacity to infect particular hosts. Similarly a host species may show distinct strains, some being susceptible to a particular fungus, and others resistant. In either case the term **biologic species** or **biologic form** is applied to the strains within a given species which differ in their capacity to infect or be infected[1]. In some cases at least immunity on the part of the host has been shown to be a recessive character in the Mendelian sense; thus, when a variety of wheat susceptible to the rust, *Puccinia glumarum*, is crossed with a resistant form, all the plants in F_1 are rusted, and three-quarters of those in F_2 also undergo infection, while the remaining quarter stand green and uninjured among them[2]. It is unfortunately not possible to ascertain whether the power of infection in the fungus is inherited in a similar way.

The resistance of a plant which is immune when healthy may be broken down by injury[3]; thus, when conidia of *Erysiphe Graminis*, growing on wheat, are sown on normal leaves of wheat and barley, the wheat may be attacked but never the barley; if the barley leaf, however, be cut or burned, and the conidia applied to the uninjured surface on the other side of the leaf, infection occurs, and the mycelium may become acclimatised upon a new host. In nature, injuries caused by insects are sufficient to destroy resistance, and in this way diseases developing on weed grasses round a field of corn may sometimes be transferred to the crop, even if not ordinarily capable of infecting it.

Heteroecism. The great majority of parasitic fungi pass through their life history in or on the tissues of a single host; such forms are said to be **autoecious** in contradistinction to the **heteroecious** forms which require two alternating hosts for the completion of their development. With the exception of the ascomycetous species *Sclerotinia Ledi*, all known heteroecious fungi belong to the rusts; they pass through their gametophytic stage

[1] Ward, 1902–5; Diedicke, 1902; Marchal, 1902–3; Marryat, 1907; Freeman and Johnson, 1911; Stakman, Piemeisel and Levine, 1918; Wormald, 1919; Sampson, 1925.

[2] Biffen, 1907, 1912; Pole Evans, 1911; Varilov, 1914; Hayes, Stakman and Aamodt, 1925.

[3] Salmon, 1904–5.

relatively early in the year, and the spores which are the immediate products of the sexual organs are incapable, in heteroecious species, of germinating on the host on which they were borne, but develop if they alight on the appropriate host of the sporophyte. Such a condition may possibly have originated as a means of prolonging the growth period where the original host of the gametophyte died down early in the year; but, in many existing cases, the host of the gametophyte continues its activity throughout the summer as in the well-known rust of wheat, *Puccinia Graminis*, the gametophyte of which occurs on the barberry.

REACTIONS TO STIMULI

The response of fungi to external stimuli can in most cases be related to the distribution of spores or to nutrition. In addition, special reactions occur in the approach and fusion of the sexual organs; in the Mucorales, directive growth is found in morphologically undifferentiated hyphae, and the formation of gametangia follows on the contact of appropriate branches. Presumably some chemical stimulus is involved here, and also in the movement of the trichogyne towards the male organ in *Zodiomyces*, and perhaps in other Ascomycetes, but nothing is known of the active substance.

Chemotaxis. The zoospores of *Saprolegnia mixta*[1] swim towards aqueous extracts of dead insects and towards aqueous solutions of their decomposition products, such as proteins, phosphates, urea and organic acids, if suitably diluted; a substance which attracts in weak solutions repels in strong ones. The zoospores are very sensitive, and will react to a solution containing 0·0001 per cent. of orthophosphoric acid, or 0·00025 per cent. of protein material. In the case of organic acids, and doubtless of some other substances, the minimum concentration which will cause response varies inversely with the degree to which dissociation takes place in solution. Similar responses are found in zoospores of other species. They have an obvious biological significance, but nothing is known of the mechanism of the reaction. Repulsion is not caused by poisonous salts; the zoospores swim readily into a solution which contains a protein and a poisonous dose of mercuric chloride.

[1] Müller, 1911.

Chemotropism. The strongest chemotropic reaction of hyphae and germ tubes is a negative one; they grow away from regions which have been staled by the products of their own metabolism[1]. A simple example of this reaction is found in the circular growth of mycelia both in nature and in artificial culture. In so far as a clear field is available, hyphae tend to grow equally in all directions from the point of infection. The same factor may account for the alternate dense and sparse zones which characterise many fungal colonies and are independent of changes in light and temperature[2]. Energetic growth results in the deposition of katabolic substances, and growth is accordingly reduced till a few hyphae pass beyond the inhibiting influence and give rise to a new ring of richly branched mycelium. In older colonies the germination of fresh spores outside the zone of staling substances doubtless adds to this effect.

Chemotropism is investigated by means of perforated mica plates coated on both sides with a suitable agar medium[3]. When spores of *Rhizopus nigricans* are sown in approximately equal numbers on both sides of such a plate, the germ tubes show no special reaction towards the holes. When, however, one side only is sown, most of the germ tubes grow towards and through the holes; in this case, as the fungus develops, the medium is staled, and the products of metabolism diffuse through the perforations into the unsown layer. Since the germ tubes tend to grow away from the staling substances, they follow the falling diffusion gradient through the holes, and find their way to the fresh medium. A heavily staled medium may be obtained by growing *Rhizopus* for some weeks in turnip juice, filtering to remove the mycelium, and adding agar. If such a medium, which has not been heated above 40° C., is contrasted with fresh turnip juice agar, and spores sown only on the latter, the germ tubes grow away from the holes, for a strong diffusion current passes from the stale to the fresh medium. This effect may be reduced by heating the stale medium to 100° C.; the germ tubes show much less tendency to avoid the holes, suggesting that heating has dissipated some of the injurious substances.

The progress of staling may be estimated by periodical measure-

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[1] Clark, 1902; Fulton, 1906; Balls, 1908; Graves, 1916; Brown, W., 1922 ii, 1923, 1925; Pratt, 1924.
[2] Stevens and Hall, 1909.   [3] Graves, 1916.

ment[1] of the diameter of a fungus colony grown on a solid medium. *Botrytis cinerea* on potato agar gives little evidence of staling; the colonies work up to a maximum rate of growth and tend to maintain it. On the other hand, species of *Fusarium* reach a maximum rate, then show a falling off, and may cease to grow before the edge of the medium is reached. *Botrytis* produces relatively little staling substance, *Fusarium* a great deal. In the latter case, the medium outside the colony becomes staled, either by the active substances diffusing outwards more rapidly than the colony grows, or by the bare region absorbing gaseous products from the atmosphere of the dish.

It is clear that renewed growth cannot be obtained by stripping the mycelium from a staled medium and reinoculating with spores. Ammonia and potassium bicarbonate are known to be among the substances which cause staling[2]; the former is driven off by heating, the latter is decomposed. These facts are in agreement with the observation that the capacity to support some growth may be restored by heating; growth has not ceased because the substratum has been exhausted of nutritive material. The staling effect may be delayed by supplying the cultures with an atmosphere of carbon dioxide, which unites with ammonia; by ventilation, so allowing the ammonia to escape; by using a large bulk of medium, so deferring the development of a concentration of staling substances sufficient to stop activity; and by cutting out the centre of the colony, thereby removing the reservoir from which diffusion takes place into the unstaled medium.

Rise of temperature accelerates the rate of chemical change; in agreement with this, staling is more rapid at high than at low temperatures[3]. In estimating the effect of temperature upon the behaviour of a fungus, it is however necessary to bear in mind that a high temperature may cause direct injury in addition to the influence exercised upon the production of staling substances, and so on the rate of growth.

There is some evidence that germ tubes and hyphae grow towards salts, sugars and other nutritive substances, and away from acids, alkalis and alcohols[4]. It is difficult to distinguish between

[1] Brown, W., 1923. [2] Pratt, 1924.
[3] Balls, 1908; Brown, W., 1922 ii.
[4] Miyoshi, 1894; Graves, 1916.

the reaction due to staling and the positive chemotropic response; the latter is always much weaker than the former, and is probably best seen when the culture is young, and the concentration of waste products low.

Aerotaxis. The zoospores of *Rhizophidium pollinis* and *Rhizophidium sphaerotheca* are extremely sensitive to free oxygen; when mounted under a coverslip they move at once to the margin of the drop, or to air bubbles in the preparation; they crowd into capillary tubes containing oxygenated water, and have a tendency to form groups around globules of turpentine, a good oxygen carrier[1].

Aerotropism. Growth in response to varying concentrations of free oxygen is rarely shown by fungi. The sporangiophores of *Phycomyces nitens*[2] bend towards pieces of iron placed close to them. Rusting iron liberates small quantities of ozone, and apparently the bending takes place in response to this. Similar curvatures may be obtained towards sheets of platinum foil, or glass, bearing adsorbed ozone.

Hydrotropism. The position perpendicular to the substratum assumed by very young sporangiophores of the Mucorales has been ascribed to negative hydrotropism. In saturated air, the sporangiophores of *Phycomyces* are oriented irregularly, and the divergence of the tufted sporangiophores of *Rhizopus* may be due to negative hydrotropism in response to transpired water, drops of which often appear in or near the region of elongation. Exposure to moist air increases the rate of growth of the sporangiophores of *Phycomyces nitens*[3]; they sometimes show weak curvatures away from wet paper placed vertically in their neighbourhood.

It is probable that vegetative hyphae grow towards moisture, but there is no conclusive evidence to show that this is so, as it is difficult to discriminate between the effect due to water, and that due to staling substances[4].

Phototaxis. The zoospores of *Rhizophlyctis vorax*[5] and of *Polyphagus Euglenae*[6] move towards the light. Both these species attack motile green organisms, the former infecting *Chlamydococcus pluvialis*, the latter, *Euglena viridis*. The hosts react to light,

[1] Müller, 1911.
[2] Elfving, 1917.
[3] Walter, 1921.
[4] Fulton, 1906; Robinson, 1914.
[5] Strasburger, 1878.
[6] Wager, 1914 i.

since they obtain their carbon supplies by photosynthesis, and the phototactic response of the parasite brings it into regions where the hosts are to be found. The zoospores of *Rhizophidium pollinis*[1] show a weak positive reaction; this is probably bound up with their need for abundant supplies of free oxygen.

Phototropism. Many fruit bodies are sensitive to light, and by means of this reaction adjust themselves in a position favourable to the distribution of their spores, the direction of light indicating the direction of open space.

The sporangiophores of species of *Pilobolus*, *Mucor* and *Phycomyces* bend towards the light. In the genus *Pilobolus*, the hemispherical sporangium is borne on an aseptate sporangiophore which develops a swelling just below the sporangium and another at its base. A new crop of sporangia matures daily, and discharge takes place in the morning or the early afternoon; growth is apical, and the tips of the young sporangiophores bend towards the source of light as they grow. An unnamed species[2] showed a recognisable curvature about thirty minutes after exposure to light in a given direction. Curvature is arrested during the early stages of the growth of the sporangium, and is resumed again when the subsporangial bulb is beginning to form; during the later stages of development, curvature takes place below the bulb, which may perceive light[3]. In this way the bulb and the terminal sporangium are pointed in the direction of light, and some accuracy of aim is secured. In a series of experiments[4] involving some 20,000 specimens, illuminated by means of apertures 1 cm. in diameter, nearly 90 per cent. of the sporangia entered the aperture or hit the walls within 1 cm. of it. When illuminated by two equal sources of light, the sporangiophores pointed to one or the other; when the sources of light differed, the sporangia were shot off in larger numbers towards the light in which the proportion of blue rays was greater.

Young sporangiophores of *Phycomyces nitens* may show curvature in fifteen minutes. Bending takes place at a point just below the developing sporangium, and elongation proceeds in a straight line towards the light. Illumination increases the rate of growth[5], so that exposure to unilateral light might be expected to produce

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[1] Müller, 1911.   [2] Jolivette, 1914.
[3] Buller, 1921.   [4] Parr, 1918.   [5] Blaauw, 1914.

a negative curvature in the sporangiophore. Apparently, however, its transparency enables the structure to act as a lens, so that light falling on one side is concentrated on the opposite side, where growth is accelerated and a positive curvature induced.

The necks of the perithecia of *Sordaria* and other Pyrenomycetes show a positive response sufficiently delicate to cause a zigzag development of the neck if the direction of light is repeatedly changed. The asci of *Ascobolus immersus* and *Ascobolus furfuraceus* are also positively phototropic so that an appropriate direction is obtained for the ejection of their large spore mass.

The well-marked positive response shown by immature fruit bodies of *Coprinus niveus* and *Coprinus curtus*, both coprophilous species, enables them to push up from the irregular substratum[1]. The stipe ceases to be phototropic when the pileus begins to expand, and develops instead a negatively geotropic reaction; by these means, the apex of the stipe is brought into the light before the growth of the pileus begins, and the latter has space for its horizontal expansion. A similar succession of reactions takes place in the development of the sporophores of *Lentinus lepideus*[1]; the young stipe is positively phototropic and in the absence of light grows straight onwards, without giving rise to a pileus; with adequate illumination a pileus appears, and, as its development proceeds, the positive response to light is replaced by a negative reaction to gravity. In *Amanita phalloides* and *Amanita crenulata* there is a positively phototropic response[2] even after the appearance of the pileus.

Psalliota campestris and *Coprinus comatus* usually appear on turf in open places; they are insensitive to light, and the adjustment of the parts is secured by negative geotropism[3].

A negatively phototropic reaction is comparatively rare. Germ tubes from the basidiospores of *Puccinia Malvacearum* and from conidia of a species of *Botrytis* turn away from unilateral light; those from the aecidiospores of *Puccinia Poarum*, and from the conidia of *Peronospora parasitica* and *Penicillium glaucum* are indifferent[4].

Formative Influence of Light. Many fungi are unable to develop in a normal manner unless they are adequately illuminated[3].

[1] Buller, 1909 ii. [2] Streeter, 1909.
[3] Brefeld, 1877; Buller, 1909 ii. [4] Robinson, 1914.

Young fruit bodies of *Polyporus squamosus*, though quite irre-
sponsive to the direction of light, fail to give pilei in continuous
darkness. The same is true of many other Hymenomycetes, in-
cluding those which, like *Lentinus lepideus*, are positively photo-
tropic. In many cases a brief period of illumination during the
early stages of development is all that is necessary; once started,
the differentiation of the pileus can be completed in the dark.
Light stimulates the development of the ascocarps of *Pyronema
domesticum* and other Ascomycetes; cultures remain sterile in dark-
ness, and fruit sparingly in dim light; on the other hand, *Eurotium
herbariorum* appears to form perithecia as readily in darkness as
in light.

Geotropism. The sporangiophores of *Phycomyces* and of *Mucor*
emerge at right angles to the substratum, grow to a length of about
2 mm. and then become negatively geotropic. The mycelia seem
to be indifferent to gravity. The fructifications of several of the
Helvellales and the stromata of *Poronia punctata*[1] and *Xylaria
Hypoxylon*[2] among the Pyrenomycetes, exhibit a negatively geo-
tropic reaction from early stages of development. The Hymeno-
mycetales show marked response to gravity. In stipitate forms the
stipe is negatively geotropic as soon as the pileus develops, though,
in species of *Coprinus*, and in *Lentinus lepideus*, this may be pre-
ceded by a phase in which light is the directive influence[3].

The geotropic response is of the nature of a gradual adjustment.
The growing stalk swings beyond the vertical line, changes its
direction and swings across it again, passing the vertical two or
three times before it comes to rest. In *Amanita crenulata*[4] the stipe
reaches its full development in about twenty-four hours; this may
not allow time for complete adjustment, so that the sporophore
may come to rest out of the vertical. In this species, the young
stipe elongates throughout its length until more than half grown;
the zone of most rapid elongation is just below the pileus, and as
growth slackens it becomes narrower and narrower. The per-
ceptive region is in the stipe, and is so sensitive that a definite
response may be obtained by placing the stipe in a horizontal
position for one minute.

In the stemless Hymenomycetes, as in the stipitate forms, the

[1] Dawson, 1900.   [2] Freeman, 1910.
[3] Buller, 1909 ii.   [4] Streeter, 1909.

orientation of the pileus takes place in response to gravity[1]. This is well shown by the horizontally arranged fruit bodies of the bracket-like species of *Thelephora*, *Stereum*, *Polyporus* and *Polystictus*.

Alike in the Hydnaceae, Agaricaceae and Polyporaceae, the trama plates of the fertile region are positively geotropic. In stemless forms this reaction is responsible for the orientation of the hymenium; it may be particularly well seen in some of the Hydnaceae, where the spines grow downward whatever the orientation of the sporophore, and it could doubtless be demonstrated also in *Tremellodon* among the Tremellaceae. In stipitate species it appears as a supplementary reaction coming into play if further adjustment is needed when the stipe is fully grown. The limitations of the method in the gill-bearing fungi are obvious, for, if the pileus is oblique and the gills undergo much curvature, they become crowded together and interfere with spore dispersal.

Formative Influence of Gravity. A young fruit body of *Polystictus cinnabarinus*[2] was rotated in a moist chamber on a horizontal clinostat for several weeks. A cushion-like structure was formed with the pores all over the surface, and with hardly any difference between the dorsal and ventral faces. This suggests that the localisation of the pores to the ventral surface under ordinary conditions is directly due to the influence of gravity.

Interaction of Stimuli. The life history of a fungus is the sum of its reactions to stimuli, and may, as a rule, be divided into three phases; a period of vegetative growth merges into one characterised by the appearance of organs of accessory multiplication, and this is followed by the development of the sexual apparatus[3]. The change from a vegetative condition is influenced by nutrition, light, temperature, aeration, moisture, and the encounter of mechanical obstacles; any of these may be the limiting factor if the remaining conditions are favourable.

Conditions which favour vegetative activity are opposed to the development of sexual organs; to a less extent, they discourage the formation of accessory spores[4]. Many fungi give rise to a vigorous mycelium on substrata rich in carbohydrates, but remain sterile,

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[1] Buller, 1909 ii.   [2] Hasselbring, 1907.
[3] Klebs, 1896–1900; Fraser and Chambers, 1907.
[4] Klebs, 1896–1900.

or bear a scanty crop of conidia; a moderate supply of carbo-
hydrates favours the formation of conidia; when the carbohydrate
is further reduced, and some source of nitrogen is present, the
sexual organs appear. *Eurotium herbariorum* is an exception[1], for
heavy crops of perithecia are obtained on a medium containing
40 per cent. of cane sugar; it may be that in this case the concen-
tration of the medium checks vegetative activity. The Phyco-
mycetes appear to be less sensitive to the presence of carbohydrates
than the Ascomycetes, but, in *Phytophthora*, an increase in the
proportion of carbohydrate may limit the development of sexual
organs. There is evidence that, although a supply of nitrogenous
food is a necessary preliminary to the formation of gametangia,
they do not appear[2] until the substratum is depleted of this
material. Rich nitrogenous manuring is stated to check the de-
velopment of the fruit bodies of Hymenomycetales growing on
soil[3]. Aquatic fungi[4] are markedly sensitive to external conditions,
and tend to form fructifications when the substratum is becoming
impoverished, or when the surrounding water is fouled by the
products of their activity and that of other organisms.

There is evidence that illumination exerts a depressing effect
upon the amount of vegetative development, which proceeds better
in the dark, but exposure to light may increase the rate of elonga-
tion[5] of individual hyphae. Mycelia grown in the dark may bear
sporangia or conidia, but the formation of the sporophores of the
higher fungi is frequently dependent on a supply of light.

The effects of heat upon the fungi are less sharply defined than
are those of most other external conditions. Spores are usually
able to resist extremes of temperature which kill the mycelium,
and the latter will grow at temperatures too high or too low[6] to
permit the formation of reproductive structures. Although it is
probable that the temperature relations of most fungi are ad-
justed to the ordinary climatic conditions of their habitat, *Clado-
sporium herbarum*[7] forms spores on meat in cold storage at $-6°$ C.,
whilst *Eurotium herbariorum* yields abundant conidia and perithecia
at $35°$ to $37°$ C.

[1] Fraser and Chambers, 1907.
[2] Robinson, 1926 ii.   [3] Gilbert, 1875.
[4] Klebs, 1896–1900; Kauffman, 1908; Obel, 1910; Lechmere, 1910–11;
Collins, 1920; Kanouse, 1925.   [5] Blaauw, 1914.
[6] Weimer and Harter, 1923.   [7] Brooks and Hansford, 1923.

Moisture may have a definite influence upon development, perhaps by regulating transpiration; in damp air, *Sporodinia grandis*[1] yields sporangia, but gives zygospores when the air is almost saturated, while under humid conditions, the stromata of *Xylaria Hypoxylon*[2] tend to break up into separate hyphae.

Mechanical obstacles, such as the sides of a Petri dish, gaps in the substratum, solid objects projecting from it, or the mycelia of other fungi, encourage the formation of organs of multiplication. Growth is checked, cytoplasm accumulates in the tips of the hyphae, and a new type of development is initiated[3]. When a growing mycelium encounters that of another fungus, the latter may act as a mechanical obstacle, or may affect nutrition by the secretion of staling products, or by changes in the composition of the substratum. *Lachnea* forms apothecia when in contact with *Penicillium* upon a medium on which it will not fruit in pure culture, and bacteria[4] have been observed to influence the fruiting of other Ascomycetes.

In some cases, at any rate, there is a relation between the rate of respiration and the formation of organs of multiplication[2]. Respiration is high in the early stages of growth, and falls as the mycelium ages; when this has happened, sporangia appear, or, if other conditions permit, sexual organs are produced. In closed Petri dishes, rings of conidiophores often appear at the margin of the culture[5], but when the culture is made in an open dish, they develop over the whole surface; this may indicate a relation to the supply of free oxygen, and so be connected with respiration.

The appearance of the organs of multiplication is accompanied by changes in the structure and contents of the cytoplasm, and, in many fungi, by the formation of definite pigments, indicating that the metabolism of the plant is undergoing a change; there is doubtless an intimate connection between this change in internal conditions and the altered behaviour of the fungus[6]. The external conditions which affect fertility do not appear to do so directly, but by modifying the chemical processes in the protoplasm; so far, these changes have defied analysis.

[1] Robinson, 1926 i. [2] Freeman, 1910. [3] Robinson, 1926 i, ii.
[4] Cf. p. 17. [5] Barnes, 1924–25.
[6] Bezssonof, 1918–19; Boas, 1918–19; Sartory, 1918; Molliard, 1920; Brown, W., 1922 ii, 1923, 1925, 1926; Leonian, 1925; Brown and Horne, 1926.

PHYCOMYCETES

The Phycomycetes include about 800 species, characterised by the aseptate vegetative thallus, which, in form, ranges from a rounded sac to a richly branched mycelium.

Accessory multiplication is by means of zoospores or non-motile spores produced in sporangia. In a number of cases, the contents of the sporangium do not separate, or are reduced to a single spore; the resultant structure functions as a conidium, germinating by the protrusion of a germ tube. Portions of the mycelium may be converted into chlamydospores by the appearance of septa, and the development of a thick wall around the segments.

Resting sporangia, oospores and zygospores are formed as the result of normal fertilisation, or of parthenogenesis.

The lowest Phycomycetes are mostly aquatic; they live as parasites on plants and animals, or, in a few cases, as saprophytes; some attack flowering plants, especially those found in wet situations. With few exceptions, their sporangia liberate zoospores. Rather more advanced species are amphibious; they occur as parasites in plants, or as saprophytes in the soil. In the presence of sufficient moisture, zoospores emerge from the sporangia, but under relatively dry conditions the latter function as conidia. The highest Phycomycetes depend upon the wind for the distribution of their spores; they include parasites in Phanerogams, a few parasites which can attack their near relatives only, and many common saprophytes; their sporangia give rise to non-motile spores, or function as conidia; zoospores are not produced.

The Thallus. It seems probable that two factors have played an important part in the evolution of the soma in Phycomycetes —the extension of the thallus in relation to the need for searching wide areas for nutritive material, and the elaboration of specialised branches on which the sporangia may be raised above the substratum, facilitating the escape of the spores. The increase in size of the thallus has brought, as a necessary consequence, a lengthening of the life of the individual, the production of a larger number of sporangia, and the assumption of the mycelial habit.

In the Archimycetes the thallus is of simple construction, and

the filamentous portion, if present, is usually weakly developed. In *Olpidium* the thallus is a rounded structure, with no appendages; it lies in the contents of the host cell, is derived by enlargement from the naked body of the zoospore, and at maturity is converted into a single reproductive organ. Increase of surface in proportion to volume, and probably, therefore, better nutritive relations, have been attained by the development of lobes, as in *Pleotrachelus*, or by elongation and branching, as in the Ancylistales. It is possible that the mycelium of *Pythium* represents a further step in this direction, with attenuation of the filaments and increase in the number of branches. The beginning of another line of development is indicated in *Rhizophidium* (fig. 14); in this genus the thallus consists of the enlarged body of the spore, attached to the outside of the host, and a scantily branched system of rhizoids which collect nutritive material. In related species the rhizoids become more important, spread over a wider area, and may attack more than one host, but the sporangium is still formed from the enlarged zoospore. However, with the increased development of the rhizoids, a tendency appears for the sporangium to form as an outgrowth from the swollen part of the thallus, as in *Polyphagus Euglenae* and *Macrochytrium botrydioides* (fig. 24 *a*). The latter may represent a link between the Chytridiales and the Leptomitaceae, through *Rhipidium americanum* (fig. 36 *a*), in which the thallus is divided into a rhizoidal system, a main axis derived from the zoospore and a crown of fertile branches. The Leptomitaceae show a decline of this type of organisation, of which some reminiscences may be preserved in the mycelium of the Monoblepharidaceae, the Saprolegniaceae and the Peronosporaceae.

The higher Phycomycetes possess richly branched hyphae, spreading on the substratum, or in the intercellular spaces of the host. Fertile branches arise in considerable numbers, and sporangia are produced over a lengthy period.

In most Phycomycetes septa appear in connection with the reproductive organs. Although the vegetative mycelium is usually aseptate, old, empty portions of hyphae are cut off by thick septa in *Pythium* and *Phytophthora*; and, in the exceptional species, *Allomyces arbuscula*, septa are formed early in the life of the plant. Septation with the formation of chlamydospores occurs in the hyphae of species of *Saprolegnia* and *Mucor*.

The Sporangium. In many Archimycetes the contents of the thallus are used up in the production of zoospores, produced in one or more sporangia. The thallus undergoes little change in form; such changes as occur are associated with the development of a mechanism for the liberation of the spores. In most Oomycetes and Zygomycetes the sporangium is terminal; it has a definite form, and is cut off from its stalk by a basal septum. In a few species of *Pythium*, however, a differentiated sporangium is not formed.

The activity of the organism may terminate in the production of one or more sporangia, or vegetative growth and the formation of sporangia may go on simultaneously. In the latter case sporangia mature in succession on the same branch system, or they ripen singly or in groups on sporangiophores developing independently from the vegetative mycelium. The development of sporangia in succession is characteristic of the aquatic and amphibious species, whilst the formation of sporangia, with no reference to those already matured, occurs in species which show little dependence upon water for the distribution of their spores.

The successive formation of sporangia may be brought about by **proliferation** of the fertile hypha, by the development of chains of sporangia, or by the building up of a sympodial system of fertile branches. Proliferation takes place by the growth of the sporangiophore through the base of the empty sporangium, and the formation of a new organ within or beyond its predecessor. This process is apparently confined to aquatic fungi; it occurs in *Harpochytrium*, *Cladochytrium* and other Archimycetes, and in a number of Oomycetes; it is especially characteristic of *Saprolegnia* (fig. 4 *a*). Basipetal chains of sporangia are formed in *Pythium*, in *Monoblepharis* and *Dictyuchus*; this arrangement reaches its highest development in the Albuginaceae (fig. 4 *b*). Sporangia are formed on sympodial branch systems in the Pythiaceae and in *Achlya* (fig. 4 *c*).

When the position of the sporangium is not influenced by that of its predecessors, a definite sporangiophore is usually present; this may remain simple and bear one sporangium, as in some Mucoraceae, or it may show dichotomy, irregular branching, or a racemose arrangement, and carry a number of sporangia.

In many aquatic and amphibious fungi the sporangium liberates

zoospores or protrudes a germ tube before it falls from the sporangiophore; when, however, there is little external water the sporangium may fall and either yield zoospores or produce a germ tube according to the amount of water present where it comes to rest. The significance of external water is much less marked in subaerial species. In such forms, in most of which sporangia are developed independently, the sporangium may no longer liberate

Fig. 4. *Saprolegnia monoica* Prings.; *a*, renewal of the sporangium by proliferation of the fertile hypha, ⤢ 225; after Pringsheim. *Cystopus candidus* (Pers.) Lév.; *b*, group of sporangiophores with chains of sporangia, ⤢ 450. *Achlya racemosa* Hildebr.; *c*, sympodium of sporangia, ⤢ 55; after Pringsheim[1].

motile spores; it either functions as a conidium, or non-motile spores are set free and dispersed by the wind. The transformation of the sporangium into a conidium is readily observed in the Peronosporaceae, and, along rather different lines, in the Choanephoraceae and Mortierellaceae.

There is a general uniformity throughout the Phycomycetes in the manner of spore formation[2]. The contents of the young sporangium include many small vacuoles; these flow together to

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[1] Pringsheim, 1873.   [2] Harper, 1899 ii; Schwarze, 1922.

form a large vacuole. In the Archimycetes[1] and Oomycetes[2] cleavage furrows proceed outwards from the large vacuole, and divide the contents into a number of uninucleate spore rudiments, which may show a tendency to round off. As this is going on, the sporangium loses water, shrinkage occurs, and the rudiments are pressed together, so that their individuality may be almost lost. Further loss of water from the contents of the sporangium is followed by the rounding off of the spores, which may now emerge. In the Zygomycetes[3] spore formation proceeds along similar lines, but, in these fungi, cleavage furrows arise at the periphery as well as in the centre, and the spores may contain more than one nucleus when they are ready for dispersal.

The spores escape through one or more exit tubes when the sporangium is buried in the substratum, or through a pore, or by the irregular tearing of the wall of the sporangium, when the latter is freely exposed. In some Archimycetes and Leptomitaceae the pore is formed by the lifting of a lid developed from the wall of the sporangium, but in most cases it appears that a weak spot in the wall is dissolved away. A few species belonging to the Archimycetes and Oomycetes discharge their zoospores by a process which seems unknown in other plants. The sporangium develops, and gives rise to a short hypha, the end of which swells to form a thin vesicle. Meanwhile, the contents of the sporangium are partially differentiated into zoospores; and the rudiments may show some movement at this stage; they pass into the vesicle, complete their development within it, and escape when it bursts. The phenomenon occurs in its full expression in *Lagenidium*[4] and *Pythium*[5]; in *Phytophthora*[6] and other genera the vesicle lasts for a short time, and may indeed burst before all the contents of the sporangium have migrated. It seems probable that this mechanism is a device for facilitating the escape of spores from an immersed sporangium; in forms with exposed sporangia the occurrence of the phenomenon may be regarded as due to the persistence of an ancestral character.

The Spore. In aquatic and amphibious species the sporangia usually give rise to zoospores; in higher Phycomycetes non-motile spores develop.

[1] Barrett, 1912 i.　　[2] Rothert, 1903; Butler, 1907.　　[3] Schwarze, 1922.
[4] Zopf, 1884.　　[5] Butler, 1907, 1913.　　[6] Rosenbaum, 1917.

The zoospores may be uniciliate, with a prominent oil drop, as in many Chytridiales, or biciliate, as in the Woroninaceae, Ancylistales, and most Oomycetes. Uniciliate zoospores are produced by *Blastocladia*[1] and related genera, and the appearance of uniciliate and biciliate zoospores in *Monoblepharis*[2], and perhaps also in *Pythium*[3], indicates that the number of cilia is not a character of fundamental systematic importance in the Phycomycetes.

The zoospores of certain Phycomycetes show two periods of activity, separated by a period of rest; this phenomenon is called **diplanetism**[4]. The zoospore of the second active period may differ from that of the first in shape, and in the manner of insertion of the cilia. Diplanetism is clearly shown by the zoospores of *Saprolegnia*. They emerge as pyriform bodies with two apical cilia, swim for a short time, withdraw their cilia, and encyst; after about twenty-four hours, a bean-shaped zoospore with two lateral cilia emerges from the cyst, and, on a favourable substratum, puts out a germ tube. Other genera of the Saprolegniaceae exhibit a gradual disappearance of diplanetism, while, in *Pythiopsis*, only pyriform spores are known. Diplanetism also occurs in the Chytridiales[5]; in these forms encystment may be replaced by the assumption of an amoeboid condition, and it is possible that in this state the zoospore ingests solid material and acquires energy to be expended on the second swimming period. In this connection a comparison may be made with the behaviour of the zoospores of the Myxomycetes[6].

Sexual Reproduction. The Phycomycetes show as great diversity in their sexual processes as they do in other respects. In the Archimycetes isogamy occurs in *Olpidium Viciae* and *Synchytrium endobioticum*; the gametes are zoospores which have been retarded in development by dry conditions. *Monochytrium Stevensianum* shows the fusion of two naked uninucleate individuals by direct contact, and in *Zygorhizidium Willei* and *Polyphagus Euglenae* uninucleate individuals unite by means of a conjugation tube, which is put out by one of them. In *Polyphagus* the contents of the two gametangia pass into a swelling formed upon the tube

[1] Thaxter, 1896 ii.   [2] Thaxter, 1895 i.   [3] Atkinson, 1894, 1909 ii.
[4] Leitgeb, 1869; de Bary, 1887; Butler, 1907; Atkinson, 1909 ii.
[5] Barrett, 1912 i; Curtis, 1921.   [6] Cf. p. 9.

produced by the smaller, an unusual state of affairs. In the Ancylis-tales antheridia and oogonia may be formed in the same or in different thalli; a conjugation tube allows the contents of the antheridium to pass into the oogonium, where the united contents of the organs round off to form an oospore. In the Oomycetes antheridia and oogonia are developed, and, in contradistinction to the conditions in the Ancylistales, one or more oospheres are formed in the oogonium before fertilisation. In *Monoblepharis* the oogonium is uninucleate from the beginning, and the nucleus does not divide; fertilisation is brought about by the entry of a motile spermatozoid through a pore in the wall. In other Oomycetes the young antheridia and oogonia are multinucleate; nuclear divisions are followed by the degeneration of many of the daughter nuclei, and the formation of one or more oospheres in the oogonia; the contents of the antheridia pass into the oospheres by means of conjugation tubes.

In the Zygomycetes sexual reproduction is by the fusion of multinucleate gametangia which grow one towards another, or are formed in contact, after the hyphae on which they develop have come together. A thick-walled zygospore is formed as the result of this process.

Phylogeny. The Zygomycetes occupy an isolated position on account of the special nature of their method of sexual reproduction, and a survey of the Archimycetes and Oomycetes brings to light no proximate ancestor of this specialised group. They may have arisen from an organism resembling *Monochytrium* in its sexual phenomena, but the absence of any intermediate link makes this a doubtful assumption.

Between the Archimycetes and Oomycetes, there are a number of points of contact[1]. In both may be observed the renewal of the sporangium by proliferation, the discharge of the partly differentiated zoospores into a vesicle, the formation of a lid in the wall of the sporangium, and diplanetism of the zoospores. Although definite lines of development cannot be laid down, there can be little doubt that the Archimycetes contain the most primitive fungi, and it seems very probable that they are the source from which

[1] de Bary, 1881 i; Thaxter, 1895 i, ii, 1896 ii, iii; Butler, 1907, 1911; Serbinow, 1907; Atkinson, 1909 ii; Petersen, 1910; Wager, 1913; von Minden, 1916; Fitzpatrick, 1923.

the higher forms have sprung. It is also probable that the Archimycetes are connected through the Olpidiaceae and the Haplosporidia[1] with the simpler Sporozoa, and by means of these, with the lower Protista[2].

The Phycomycetes may be divided as follows:

Mycelium rudimentary or obsolete	ARCHIMYCETES
Mycelium well developed	
Sexual reproduction by oospores; accessory spores often motile	OOMYCETES
Sexual reproduction by zygospores; accessory spores non-motile	ZYGOMYCETES

ARCHIMYCETES

The Archimycetes include about 350 species, most of which are parasites attacking freshwater and marine algae, aquatic animals, or land plants; saprophytes are few in number.

In the lower members of the group the thallus is a rounded, elongated or lobed structure, formed by the enlargement of the contents of the zoospore. It bears no appendages, and, when growth ceases, is converted into one or more reproductive organs. In relatively advanced forms, rhizoids assist in nutrition but take no part in the construction of the reproductive apparatus; still higher types possess a mycelium, which usually consists of tapering filaments comparable with the rhizoids of the lower forms rather than the hyphae of the higher fungi.

The Archimycetes may be divided into three alliances, to the first of which most of the species belong:

Vegetative body variable in form, used up in the production of one or more sporangia or sexual organs; zoospores usually uniciliate	CHYTRIDIALES
Vegetative body a stout filament, transformed at maturity into a row of reproductive organs; zoospores biciliate	ANCYLISTALES
Vegetative body a mycelium with terminal or intercalary resting sporangia; spores non-motile	PROTOMYCETALES

[1] Caullery and Mesnil, 1905.

[2] Dangeard, 1886; Chatton, 1908; Leger, 1908, 1914; Chatton and Brodsky, 1909; Chatton and Roubaud, 1909; Leger and Duboscq, 1909; Leger and Hesse, 1909, 1923; Robertson, 1909; Nemec, 1911 i, iv, 1913 i; de Beauchamp, 1914; Dunkerly, 1914; Neresheimer and Clodi, 1914; Cavers, 1915; Pascher, 1918; Ashworth, 1923.

CHYTRIDIALES

In the Chytridiales the thallus is at first unicellular, and either naked or walled; it may have the form of a rounded, elongated or irregular sac lying in the protoplasm of the host, and without filamentous appendages; it may be a rounded, flask-shaped or elongated body, lying within the host or attached to its surface, and bearing a system of rhizoids; or the filamentous portion may become the most obvious part of the thallus, and a basal nutritive region and an apical reproductive region be differentiated.

Zoosporangia may be formed from the whole of the thallus; they may arise from the sac-like portion only, with subsequent degeneration of the rhizoids, or they may develop as swellings on the filaments. Sporangia immersed in the host liberate their zoospores through one or more exit canals or papillae; when the sporangium lies on the substratum, the zoospores usually emerge through a simple pore.

In most genera the zoospore is spherical, with one cilium, the activity of which causes a jerky motion; the spore contains a single nucleus and a prominent oil drop. Biciliate zoospores occur in the Woroninaceae. In the lower forms the zoospore is naked, and passes as a whole into the host cell; in more advanced forms the zoospore develops a wall before the host is infected; the wall is left behind when the contents of the spore of an endoparasite pass into the host, but in ectoparasites it expands and forms the wall of the sporangium.

Diplanetism is shown in the zoospores of *Olpidiopsis*[1], *Pseudolpidium*[2] and *Synchytrium*[3] by the interpolation of an amoeboid phase between the periods of motion by means of cilia.

Resting sporangia are formed in similar situations to zoosporangia; they usually resemble the latter in form, but differ in the possession of a thick, two-layered wall, often bearing warts or spines. In a few species the resting sporangium has been found to develop after a sexual process, but, in most cases, the manner of origin is unknown. Isogamy occurs in *Olpidium Viciae*[4] and in *Synchytrium endobioticum*[3], in both species by the fusion of zoospores functioning as gametes. The union of two individuals

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[1] Barrett, 1912 i.   [2] Butler, 1907.
[3] Curtis, 1921.   [4] Kusano, 1912.

occurs in *Monochytrium Stevensianum*[1], *Olpidiopsis vexans*[2], *Zygorhizidium Willei*[3], *Polyphagus Euglenae*[4], and other species[5].

The Chytridiales include the following families:

Thallus at first naked and amoeboid, usually becoming
  walled in the course of growth, never constituting
  a mycelium

  Thallus soon becoming walled, clearly distinct from
   the contents of the host cell. Zoospores uniciliate

    Thallus entirely transformed into a single re-
    productive structure   OLPIDIACEAE
    Thallus yielding a sorus of zoosporangia, or a
    resting sporangium   SYNCHYTRIACEAE

   Thallus not clearly distinct from the contents of the
   host cell. Zoospores biciliate   WORONINACEAE

Thallus walled from the beginning and differentiated into
  a fertile and a mycelial portion, the latter generally
  feebly developed and ephemeral

  Mycelium delicate

    Mycelium appearing as a system of rhizoids
    attached to the sporangium   RHIZIDIACEAE
    Mycelium richly branched and spreading, with
    terminal or intercalary swellings   CLADOCHYTRIACEAE

   Mycelium coarse, divided into a main axis, and a
   system of rhizoids; sporangia terminal on lateral
   branches   HYPHOCHYTRIACEAE

OLPIDIACEAE

The Olpidiaceae are parasites in freshwater and marine algae, in higher plants, and in animals; they are distinguished by the sac-like or lobed thallus, formed by the enlargement of the contents of the zoospore, and entirely transformed at maturity into a reproductive structure.

The uniciliate zoospore of *Olpidium Viciae*[6] (fig. 5 *a*) swims for a time, till it comes into contact with a stem or leaf of *Vicia unijuga*. After a period of amoeboid movement, during which the cilium is withdrawn, a wall is formed and an infection tube conveys the contents of the zoospore into an epidermal cell, where they accumulate as a naked, spherical mass; this enlarges, nuclear divisions

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[1] Griggs, 1910.   [2] Barrett, 1912 i.   [3] Loewenthal, 1904.
[4] Nowakowski, 1876; Dangeard, 1900; Wager, 1913.
[5] Serbinow, 1907; Petersen, 1903, 1910.
[6] Kusano, 1912.

occur, and growth proceeds until all the available space is occupied. As growth slackens a wall forms around the thallus, and, with suitable temperature and adequate moisture, zoospores are organised from the contents, so that the thallus is converted without change of form into a zoosporangium. One or more exit canals pass from the sporangium to the exterior of the host (fig. 5 b, c), their tips become gelatinised, they burst, and the zoospores escape.
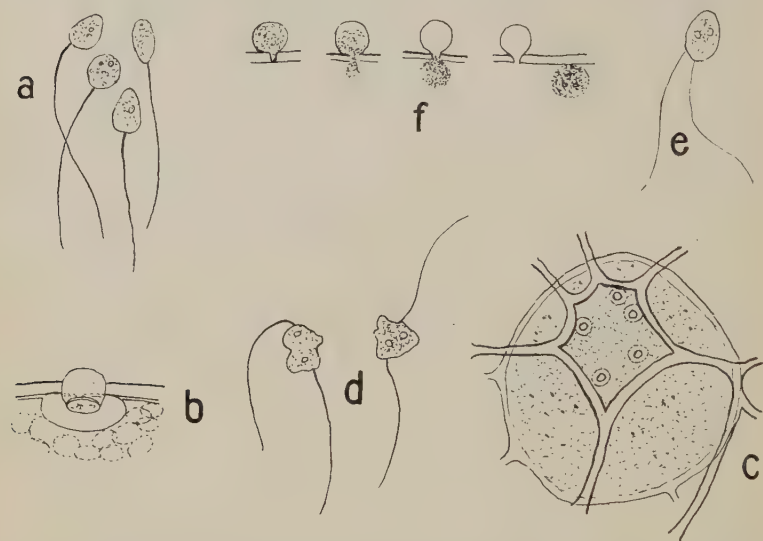
Fig. 5. *Olpidium Viciae* Kusano; *a*, zoospores, $\times$ 800; *b*, swollen exit tube, about to rupture; *c*, subepidermal host cell containing a zoosporangium with five exposed exit tubes in surface view; *d, e*, biciliate zygote, $\times$ 800; *f*, successive stages in the invasion of a cell by a zygote, $\times$ 800; all after Kusano.

The formation and escape of the zoospores are hindered when the surface of the host is dry; zoospores which have been checked by this cause may still emerge if the drought is not prolonged for more than a few days. Such retarded zoospores show a marked tendency to fuse in pairs (fig. 5 d); a biciliate zygote is formed (fig. 5 e); it swims for a time, and invades a host cell (fig. 5 f), just as a zoospore does. Apparently the two nuclei remain distinct as the zygote grows, and fuse later, when it has become a thick-walled sporangium, capable of prolonged rest. Under suitable conditions this resting sporangium gives rise to zoospores which do not appear to differ from those liberated from ordinary sporangia.

Olpidium Brassicae[1] (fig. 6) occurs in the roots of cabbages, often associated with *Plasmodiophora Brassicae*; the life histories

Fig. 6. *Olpidium Brassicae* (Wor.) Dang.; *a*, sporangia, × 160; *b*, resting sporangia, × 520; after Woronin.
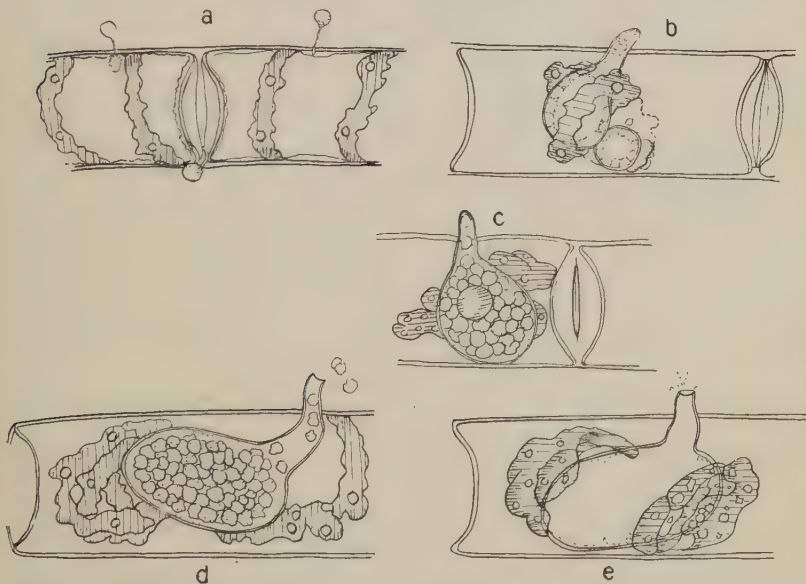
Fig. 7. *Olpidium* sp., in *Spirogyra*; *a*, zoospores invading the host; *b*, young sporangia with central vacuole; and zoospores in course of formation; *c*, sporangium about to discharge zoospores; *d*, escape of the zoospores; *e*, empty sporangium; all × 150.

of the two organisms have sometimes been confused. *Olpidium Brassicae* forms zoosporangia with single exit canals; no sexual process is known.

[1] Woronin, 1878; Favorsky, 1910; Nemec, 1912.

Other species of *Olpidium* (fig. 7) attack *Spirogyra* and other filamentous algae.

Small, uninucleate, amoeboid bodies, the **amoebulae** of *Monochytrium Stevensianum*[1], occur in the superficial cells of *Ambrosia artemisifolia*; they associate in pairs, cytoplasmic fusion follows, and the binucleate zygote enlarges rapidly, assumes a wall, and passes into a resting stage. Amoebulae which fail to fuse show
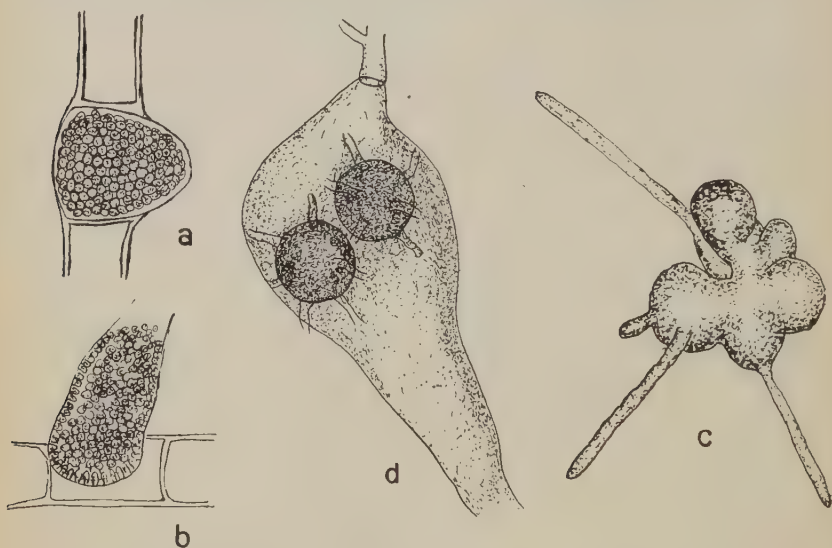
Fig. 8. *Eurychasma Dicksonii* (Wright) P. Magn.; *a*, developing sporangium in cell of *Ectocarpus*; *b*, liberation of zoospores. *Pleotrachelus Pollagaster* Petersen; *c*, lobed sporangium with four exit canals. All × 180; after Petersen. *Pleotrachelus fulgens* Zopf; *d*, two empty sporangia in aborted sporangiophore of *Pilobolus crystallinus*, × 250; after Zopf.

active growth accompanied by nuclear division; their contents finally break into a number of bodies which are assumed to be zoospores; these have not been observed free from the sporangium.

Eurychasma Dicksonii[2] (fig. 8 *a*, *b*) attacks members of the Ectocarpales. The zoosporangia develop as in *Olpidium*, but no exit tube is formed; the soft cell wall of the host is ruptured, the zoosporangium bulges through the rent, and the zoospores escape from a small papilla.

[1] Griggs, 1910.   [2] P. Magnus, 1905; Petersen, 1905.

The simpler species of *Pleotrachelus*[1] differ from *Olpidium* principally in the constant presence of several exit canals on the zoosporangium; other species have much-lobed sporangia (fig. 8 *c*), with an exit canal to each lobe. Most species attack marine algae, but *Pleotrachelus fulgens*[2] (fig. 8 *d*) is a parasite in *Pilobolus Kleinii*. It is likely that *Ectrogella Bacillariacearum*[3] is closely related to *Pleotrachelus*; it lives in diatoms, and the elongated zoosporangium with two opposite linear series of exit canals is moulded to the form of the host.

The Olpidiaceae include a number of species found in animals; *Sphaerita endogena*[4] lives in Rhizopoda; *Rhinosporidium Seeberi*[5] causes polypoid tumours in man; *Dermocystidium pusula*[6] is found in small swellings on the gills of trout and the skin of newts. These species, with others[7] less well known, may be intermediate between the rest of the Olpidiaceae and the Sporozoa.

Synchytriaceae

The thallus of the Synchytriaceae is at first naked; it soon becomes surrounded by a delicate wall, and the parasite is always visible within the cell of the host as a whitish, yellow or red sphere. At maturity a resting sporangium, or a sorus of sporangia, is formed. The zoospores are uniciliate.

The genus *Synchytrium*[8] contains a number of parasites in mosses, ferns and angiosperms; host plants in wet places are specially liable to attack. Epidermal cells are commonly entered, and, in general, cells containing chlorophyll are avoided; entrance may take place through the cell wall or by means of a stoma. Warts and other deformations appear on infected plants.

The most completely investigated species is *Synchytrium endobioticum*[9], the cause of wart disease in potato. The naked zoospore enters a young host cell, at or near ground level, and passes to the base of the cell, where it rounds off, enlarges, and forms a wall of

[1] Petersen, 1905.   [2] Zopf, 1884.

[3] Zopf, 1884; Petersen, 1905.

[4] Dangeard, 1886; Chatton and Brodsky, 1909.

[5] Ashworth, 1923.   [6] de Beauchamp, 1914; Dunkerly, 1914.

[7] Caullery and Mesnil, 1905; Chatton, 1908; Chatton and Roubaud, 1909; Leger and Duboscq, 1909; Leger and Hesse, 1923.

[8] de Bary and Woronin, 1863; Ludi, 1901; Tobler, 1913.

[9] Curtis, 1921.

two layers. In the meantime the single nucleus increases to an enormous size, and proceeds to give off stainable material into the cytoplasm[1]. A pore opens in the outer layer of the wall, and the contents emerge in a sac (fig. 9 *a*), furnished by the expanding inner layer; nuclear division begins during migration, and, when about thirty-two nuclei are present in the sac, cleavage planes are indicated by the appearance of small vacuoles. Walls are laid down
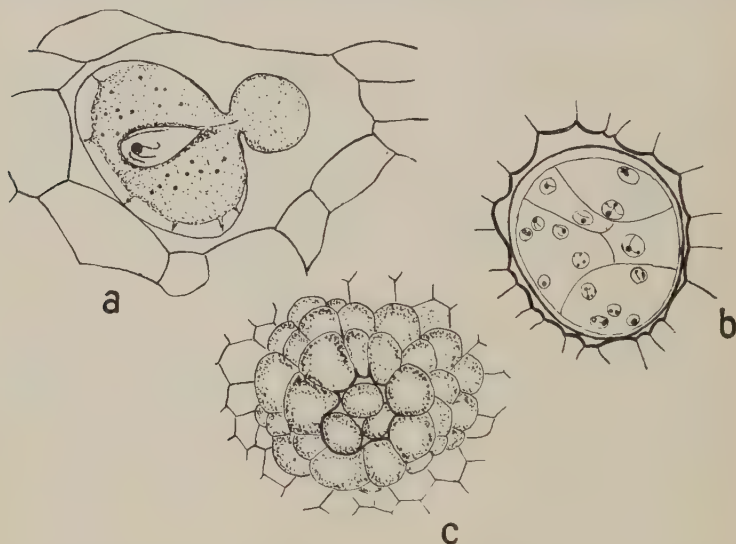
Fig. 9. *Synchytrium endobioticum* (Schilb.) Perc.; *a*, early stage in migration of the contents of the vegetative body, in preparation for the formation of the sorus; *b*, sorus of five sporangia shortly after the formation of the cleavage membranes; both × 400; *c*, surface view of mature sorus, × 170; all after Curtis.

along these planes, cutting out four or five walled sporangia which lie within the expanded inner layer of the original wall (fig. 9 *b*). In these, nuclear division continues until each contains two or three hundred nuclei, around which zoospores are organised. The mature sori absorb water and swell, the envelope of the sorus and the wall of the host cell are ruptured, the sporangia are forced out, lie free on the surface of the host, and liberate zoospores through one or more indistinctly formed papillae, or through casual slits.

[1] Stevens and Stevens, 1903; Stevens, 1907; Bally, 1912–19; Rytz, 1917; Curtis, 1921.

As in *Olpidium Viciae*, water supply is of great importance; the zoospores may be induced to function as gametes by withholding water, so that they grow old before they escape. Such zoospores swim for a time, come together in pairs, and fuse. A naked biciliate zygote is formed; its nuclei unite, it invades a cell of the host, and there gives rise to a large, walled, resting sporangium. Mitosis occurs[1], and finally a number of zoospores are set free, resembling those formed in ordinary sporangia.

A cell invaded by a zoospore enlarges somewhat as the parasite develops; at the same time the neighbouring cells elongate and divide, and a raised rosette appears around the infected cell (fig. 9 *c*) which comes to lie at the base of a funnel-shaped depression. Cells of a rosette may also be entered by zoospores, with consequent alterations in form; these changes, together with abnormal divisions in diseased tissue, lead to the formation of large galls. Cells invaded by zygotes are stimulated to tangential division, and, as the zygote lies at the base of its host cell, the resting sporangia are buried in the warts.

In some other species of *Synchytrium*[2] resting sporangia alone are known. From these zoospores may be directly produced, or there may be formation of a sorus of sporangia, either within the resting sporangium or outside it.

WORONINACEAE

The Woroninaceae are parasites of the Saprolegniales, and of *Pythium*. The thallus is at first naked, and difficult to distinguish from the contents of the host cell in which it lies; there is some evidence[3] that, as growth proceeds, the thallus may be cleft into a number of portions, each capable of independent vegetative development. At maturity, a single zoosporangium, or a resting sporangium, is formed from each vegetative unit; frequently the sporangia are associated in groups as a result of cleavage during growth, but the sori are not enclosed in a common envelope as in the Synchytriaceae. The zoospores are biciliate.

The species of *Olpidiopsis*[4] attack members of the Saprolegniales, often causing deformation of the hyphae of the host (fig. 10 *a*). The uninucleate zoospore is rounded, with two anterior cilia of

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[1] Welsford, 1921.   [2] Woronin, 1868.
[3] Serbinow, 1907.   [4] Zopf, 1884; Barrett, 1912 .

about the same length, attached close together. It swims for a time, comes to rest, the cilia shorten and again lengthen, and the zoospore resumes activity; after a time entrance is effected into a hypha of the host and the contents of the zoospore become intimately associated with those of the host. The parasite grows rapidly, nuclear divisions occur, and, towards the end of the vegetative period, a wall is formed and the whole thallus is transformed into a zoosporangium, as in *Olpidium*; the zoospores escape into the surrounding water through one or more exit tubes.

Fig. 10. *Olpidiopsis* sp.; *a*, empty sporangia in swollen filament of *Saprolegnia*; after Cornu. *Olpidiopsis luxurians* Barrett; *b*, mature resting sporangium with two empty antheridia attached; after Barrett.

In old cultures in foul water, a sexual process occurs. Two individuals of different size develop side by side; the smaller becomes firmly attached by its smooth cellulose wall to the rough wall of the larger; both are multinucleate. The contents of the smaller, the antheridium, pass into the larger, the oogonium, through a pore in the adjacent walls. The nuclei form irregular groups, and fusions probably follow. Within the

Fig. 11. *Pseudolpidium gracile*; sporangia and resting sporangia in swollen filaments of *Pythium*, × 300; after Butler.

wall of the oogonium, a thick endospore forms; it encloses an outer zone of finely granular material and a central mass of coarser granules with one or more oil drops. Nothing is known of the fate of this resting structure, to which the empty antheridium remains firmly attached (fig. 10 *b*).

The species of *Pseudolpidium*[1] also attack fungi; resting structures with spinous envelopes (fig. 11) are formed, but, in contradistinction to those of *Olpidiopsis*, they do not bear an empty antheridium.

The close association of the protoplasm of the parasite and host is especially marked in the species of *Pleolpidium*[1], *Rozella*[2] and
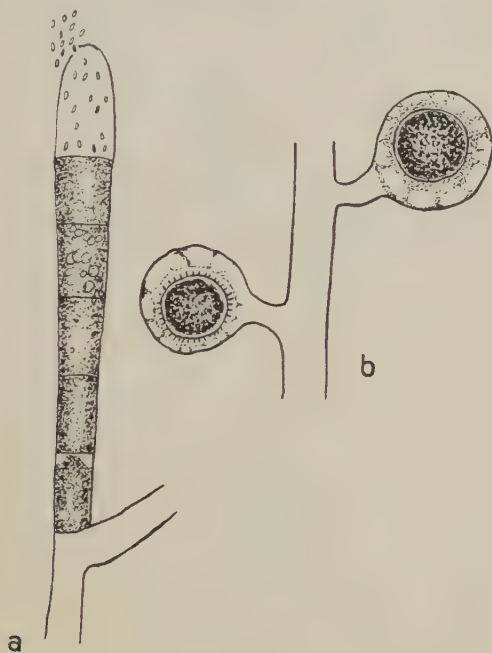
Fig. 12. *Rozella septigena* Cornu; *a*, zoosporangia in a linear series in a filament of *Achlya polyandra*, ╱ 170; *b*, resting sporangia in outgrowths from a hypha of *Saprolegnia spiralis*, × 340; both after Cornu.

Woronina[2]. *Pleolpidium* attacks *Pythium*, and particularly those species which live in the soil. The hyphae of the host undergo considerable deformation. The parasite gives rise to a single zoosporangium, which in *Pleolpidium inflatum* may be visible to the naked eye, and may contain some 7000 zoospores. *Rozella* and *Woronina* are parasites in members of the Saprolegniales; they form sori of sporangia. In *Rozella septigena* (fig. 12) the sori are

[1] Butler, 1907.   [2] Cornu, 1872.

linear, lying in the little altered hyphae of the host; *Woronina polycystis* forms groups of sporangia (fig. 13 *a*), and large resting structures, which may occupy peculiar swellings of the hyphae of the host (fig. 13 *b*).

Fig. 13. *Woronina polycystis* Cornu; *a*, sorus of sporangia in the host filament, × 340; *b*, resting sporangia in swollen hyphae of *Achlya racemosa*, × 140; both after Cornu.

Rhizidiaceae

Most of the Rhizidiaceae are parasites on aquatic organisms; a few occur within their hosts, and a few are saprophytes. The thallus is walled from the beginning; in the simpler forms it consists mainly of the enlarged zoospore, with a feebly developed mycelium; more elaborate species have a wide spread mycelium of thin, tapering filaments. Few members of the family have been investigated in detail.

The species of *Rhizophidium*[1] (fig. 14) occur on unicellular and filamentous algae, on oospores of Oomycetes[2], and on pollen grains and other vegetable material in water. A zoospore comes to rest on the substratum and penetrates it by means of a germ tube; the body of the zoospore, already clothed in a wall, enlarges to form a zoosporangium, or a resting sporangium; the germ tubes may remain simple, or may give rise to a branched system of rhizoids; in the latter case, the germ tube forms the most obvious part of the mycelium. A septum is not formed between the sporangium

[1] Zopf, 1884; Atkinson, 1909 i, ii.   [2] Melhus, 1914.
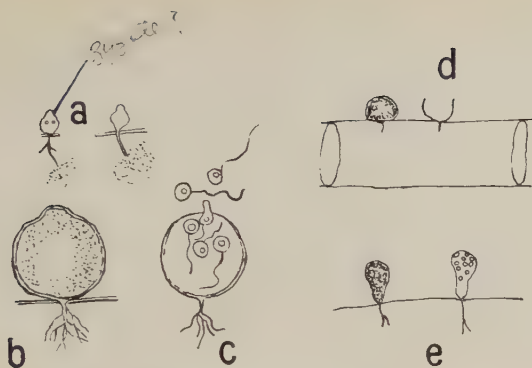
Fig. 14. *Rhizophidium brevipes*; *a*, zoospores invading the host; *b*, mature zoosporangium with rhizoids; *c*, escape of the zoospores; all after Atkinson. *Rhizophidium sphaerocarpus* (Zopf) A. Fischer; *d*, mature and empty sporangium; *Rhizophidium septocarpoides* Petersen; *e*, two sporangia; both after Petersen.
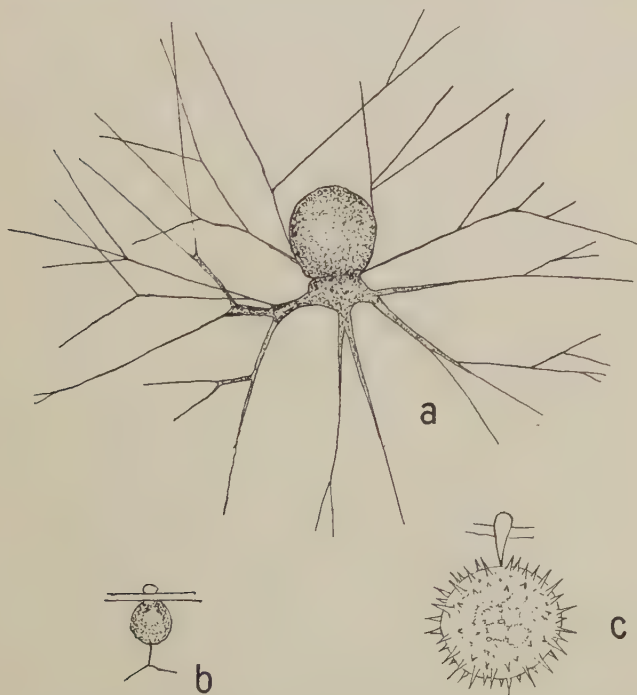
Fig. 15. *Rhizoclosmatium globosum* Petersen; *a*, mature plant. *Phlyctochytrium stellatum* Petersen; *b*, mature plant; *c*, resting sporangium. All after Petersen.

and the rhizoids, and, when the former is completely developed the latter die. The zoospores usually escape through one or more pores in the wall of the sporangium; cytological details are lacking, as well as information as to the conditions which determine the production of the resting sporangia.

Rhizoclosmatium globosum[1] (fig. 15 *a*) and *Asterophlyctis sarcoptoides*[1] live on the empty chrysalis cases of aquatic insects. In each there is a swelling at the point where the rhizoidal system springs from the base of the zoosporangium; in the latter species, the zoospores emerge from a pore at the base of the sporangium, close
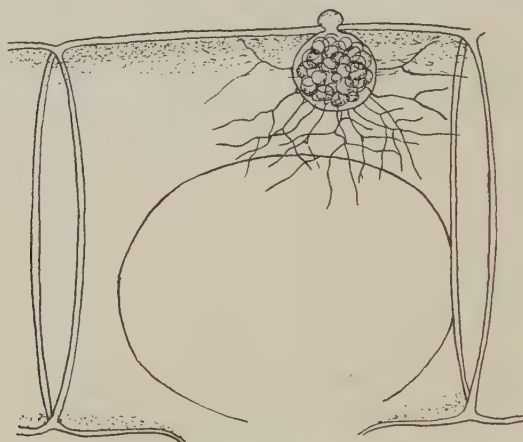
Fig. 16. *Entophlyctis bulligera* (Zopf) A. Fischer; ripe sporangium in *Spirogyra*, × 540; after Zopf.

to the subsporangial swelling. In *Phlyctochytrium stellatum* (fig. 15 *b*) the subsporangial swelling is more pronounced, and sometimes zoospores are formed within it, as well as in the sporangium proper, which is derived from the enlarged body of the zoospore[2]. The tendency for the sporangium to be formed from part of the mycelium, and not from the body of the zoospore, finds its full expression in *Entophlyctis bulligera*[3] (fig. 16), a parasite of *Spirogyra*; in this species a zoospore settles on the outside of the host and produces a germ tube in the usual way. The contents of the spore pass into the host cell, and a sporangium is formed by the swelling of a portion of the germ tube; the sporangium,

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[1] Petersen, 1903, 1910.   [2] Petersen, 1910.   [3] Zopf, 1884.

unlike those of the species hitherto considered, bears branching systems of rhizoids arising from several points on its surface.

Rhizidiomyces apophysatus[1] (fig. 17) attacks the oogonia of *Achlya*; the zoospore germinates outside the host, and forms a flask-shaped sporangium bearing a subsporangial swelling and a branching system of rhizoids. After the zoospores are partly differentiated, the sporangium puts out a tube, at the end of which a

Fig. 17. *Rhizidiomyces apophysatus* Zopf; sporangia on an oogonium of *Achlya*, × 540; after Zopf.

vesicle is formed; into this the contents of the sporangium pass, and here the development of the zoospores is completed; they escape by the rupture of the vesicle.

Harpochytrium hedeni[2] (fig. 18) is attached by a small foot to a filament of one of the green algae; the sporangium is long and narrow, and is cut off by a transverse wall from a small stalk cell. After the zoospores have emerged, a second sporangium develops within the old one by proliferation of the stalk cell; this process may be repeated several times.

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[1] Zopf, 1884; Coker, 1923.　　　　[2] Atkinson, 1903.
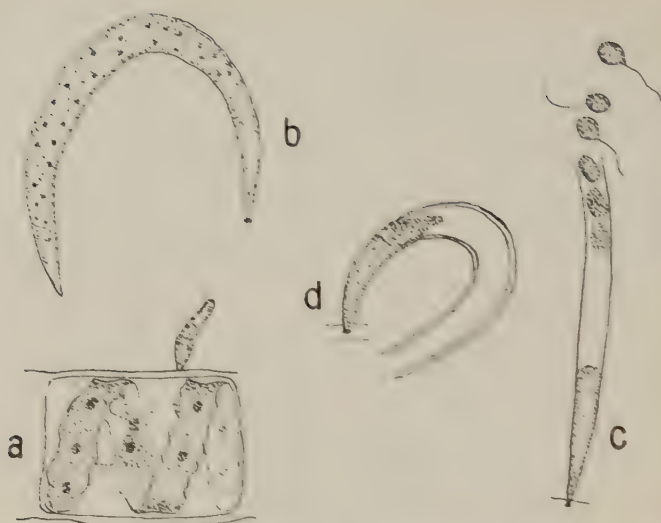
Fig. 18. *Harpochytrium hedeni* Wille; *a*, young plant on *Spirogyra*; *b*, mature plant; *c*, escape of the zoospores; *d*, old plant, with two empty sporangia and a third in course of formation; after Atkinson.
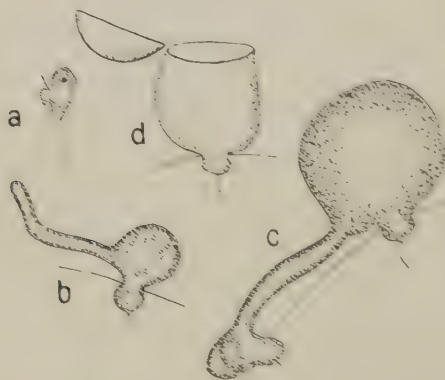
Fig. 19. *Zygorhizidium Willei* Loewenthal; *a*, zoospore invading the host; *b*, male plant with lateral branch; *c*, conjugation; *d*, empty sporangium, with lid; all × 1800; after Loewenthal.

The zoospores of *Zygorhizidium Willei*[1] (fig. 19 *a*) settle upon *Cylindrocystis*; they may give rise to zoosporangia in the usual way, with division of the nuclei occurring as growth proceeds, or they may enlarge, but remain uninucleate. Conjugation takes place between two uninucleate individuals; one puts out a lateral filament (fig. 19 *b*), by means of which its contents are transferred to the other, which is generally larger (fig. 19 *c*). A thick-walled zygote is formed, the subsequent fate of which is unknown. Zoosporangia
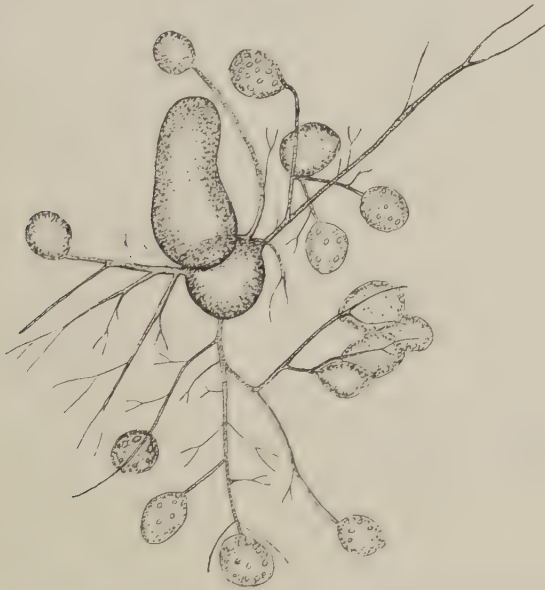
Fig. 20. *Polyphagus Euglenae* Nowak.; mature plant attached to fourteen Euglenae, and bearing a young sporangium, ╱ 320; after Nowakowski.

bearing lateral hyphae have been observed; this suggests that zoospores may be formed if fusion does not occur, even though preparations for conjugation have been entered upon. In *Zygorhizidium*, the zoospores escape by means of a lid formed from part of the wall of the sporangium (fig. 19 *d*); a similar method of dehiscence is encountered in *Chytridium Olla*[2], another member of the Rhizidiaceae.

[1] Loewenthal, 1904.   [2] de Bary, 1887.

Polyphagus Euglenae[1] is sometimes abundant on the resting stages of *Euglena* occurring on sewage beds; it does not appear to be frequent on *Euglena* from farmyards. The zoospore develops a wall and gives rise to a richly branched haustorial system (fig. 20); contact is made with many cells of the host by the ends of the filaments. At this stage the thallus is uninucleate and aseptate, and the enlarged body of the zoospore is its most prominent feature. Its contents pass into an outgrowth, a basal wall separates this sporangium from the empty vegetative body, and, after many nuclear divisions have occurred in the sporangium, zoospores escape through an apical pore.

In old cultures a sexual process takes place. As before, the thallus consists of the enlarged body of the zoospore, with a branching haustorial system; a single nucleus is present. The preliminary stages of conjugation resemble those in *Zygorhizidium*, but, in *Polyphagus*, a swelling is formed on the conjugation tube, close to the point of contact with the larger gametangium. The contents of the smaller gametangium migrate into the swelling, where they are joined by those of the larger (fig. 21), and the zygote becomes covered by a thick wall, which may be smooth or spinous. After
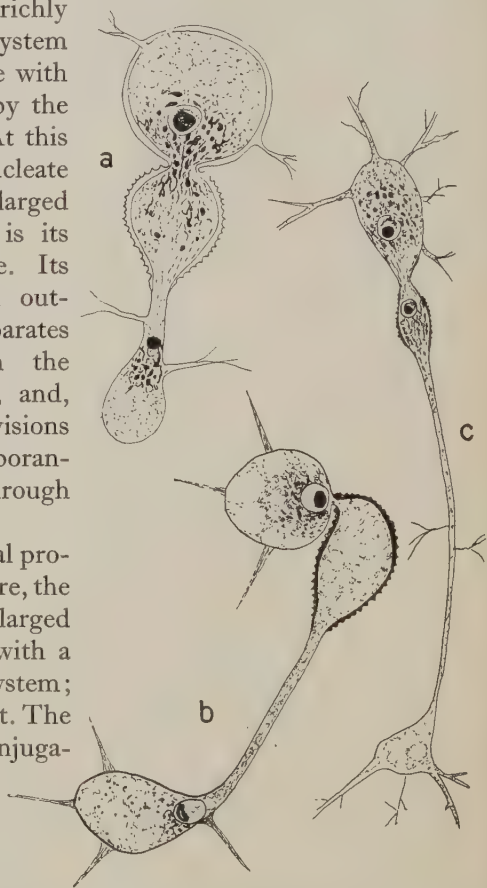
Fig. 21. *Polyphagus Euglenae* Nowak.; *a, b*, stages in formation of the conjugation tube and zygote; *c*, young zygote containing male nucleus; after Wager.

[1] Nowakowski, 1876; Dangeard, 1900; Wager, 1913.

a resting period of some months, during which the nuclei remain distinct, the zygote puts out a branch, into which the contents pass; this is a sporangium. In it the two nuclei fuse; many divisions follow, and zoospores are set free; in *Polyphagus*, nuclear divisions occur only in the sporangium[1], never in the vegetative thalli or in the zygotes.

The direct contribution to the formation of the wall of the zygote which is made by the more active gametangium of *Polyphagus* is a point of special interest, as the initiation of the sexual process and the protection of the resultant zygote are usually carried out by different participants. The functions which characterise male and female gametes in other organisms, however, are not necessarily distinctive of the gametangia, and here it is gametangia which fuse.

There is evidence of a sexual process by the conjugation of two individuals in *Siphonaria variabilis*[2] and *Sporophlyctis rostrata*[3]; in the latter non-motile spores are usually discharged from the sporangium.

Cladochytriaceae

The Cladochytriaceae are for the most part parasites in higher plants. The mycelium is strongly developed, and, as in the Rhizidiaceae, the filaments taper to delicate ends. Zoosporangia and resting sporangia are formed, often as terminal or intercalary swellings on the mycelium.

In *Cladochytrium Alismatis*[4] a zoospore comes to rest on a leaf of *Alisma Plantago* and invades an epidermal cell by means of a germ tube. Subsequent events follow one of two courses. The body of the zoospore may become a sporangium, resting on the outside of the host, and cut off by a septum from the rhizoids developed from the germ tube (fig. 22 *a*). After the escape of the zoospores, a second sporangium may be formed within the first by proliferation of the apex of the rhizoidal system; this may occur several times (fig. 22 *b*).

Alternatively, all the contents of the zoospore pass into the enlarged end of the germ tube within the host. The swelling is

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[1] Wager, 1913.   [2] Petersen, 1903, 1910.
[3] Serbinow, 1907.   [4] Clinton, 1902.

divided by a transverse wall, and the distal segment undergoes further division into a number of cells, from each of which a filament arises, passes into a fresh cell of the host, and gives rise to a similar apparatus. In the meantime rhizoids grow out from the proximal segment, and, when these have absorbed nourishment from the host cell, a lateral outgrowth appears from the proximal segment, and is converted into a resting sporangium. When this is about to liberate zoospores, a lid is formed from the upper part of the outer layer of the thick wall; the swelling of the
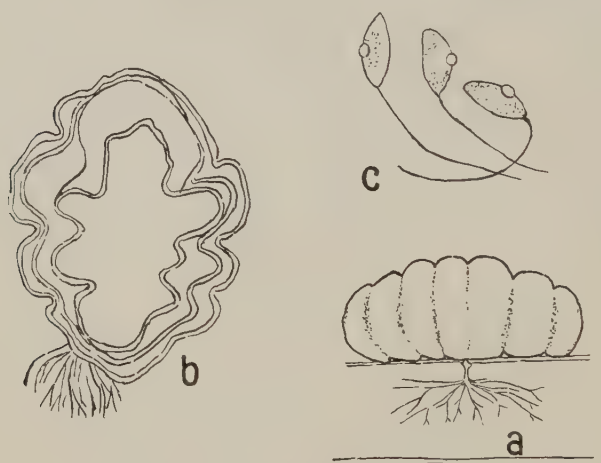
Fig. 22. *Cladochytrium Alismatis* Büsgen; *a*, sporangium and rhizoids in lateral view, × 550; *b*, renewal of the sporangium by proliferation, × 550; *c*, zoospores, × 850; after Clinton.

contents lifts the lid, the inner layer of the wall protrudes as a thin sac, and the zoospores escape from a small papilla.

Urophlyctis alfalfae[1] causes galls at or below soil level, on lucerne. The contents of the zoospore pass into a host cell, and collect there in a top-like body, surrounded by a wall. Oblique walls cut off a number of uninucleate peripheral segments, leaving a multinucleate central region. Each peripheral cell gives rise to a filament which passes into a neighbouring host cell, and bears a top-shaped swelling (fig. 23 *a*). Segmentation occurs, and the whole series of events is repeated. Meanwhile, the multinucleate

[1] Jones and Dreschler, 1920.

central region gives rise to an apical outgrowth into which nuclei
and cytoplasm pass. A crown of short, branched haustoria appears
as the outgrowth enlarges, material is absorbed from the host cell,
and a resting sporangium is ultimately formed; when this is ripe
a ring of scars indicates the points of insertion of the haustoria.
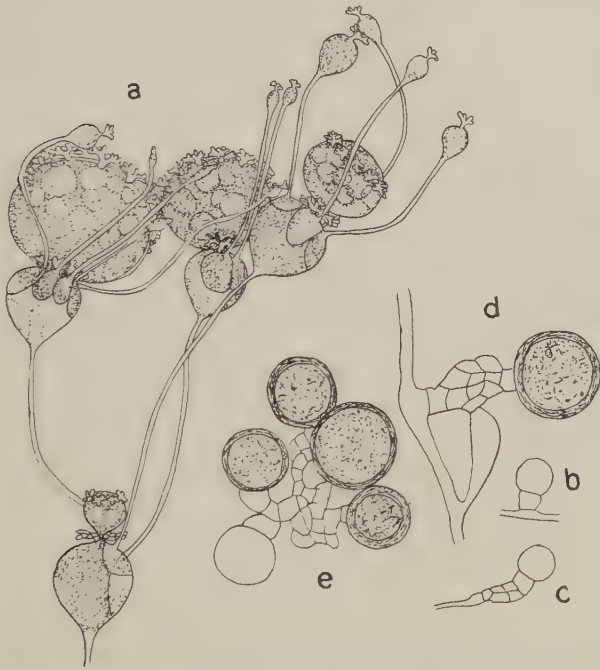
Fig. 23. *Urophlyctis alfalfae*; *a*, portion of thallus dissected from the host, showing
top-shaped cells and resting sporangia, × 680; after Jones and Dreschler.
Nowakowskiella ramosa Butler; *b*, *c*, early stages in the formation of the resting
sporangia; *d*, *e*, resting sporangia attached to a pseudoparenchyma; after Butler.

A sexual process has not been observed in these genera. It may
be that the rather complex life history of *Cladochytrium Alismatis*
is to be explained by assuming, that, as in *Synchytrium endobio-
ticum*, the zoospores are facultative gametes. If that be so, the
simple zoosporangium forms when the host is attacked by a
zoospore, and the mycelium with resting sporangia when a motile
zygote is the invader; at present, however, proof of this explana-
tion is lacking.

Nowakowskiella ramosa[1] attacks wheat plants floating in water. A swollen basal region bears eight to ten main hyphae, branching irregularly and often anastomosing. Terminal pyriform swellings appear on the hyphae, a transverse wall forms, and the distal segment becomes a sporangium. A lid is formed from the outer layer of the wall, the inner layer of the wall protrudes as a papilla, and the zoospores emerge. Within the host, the ends of hyphae
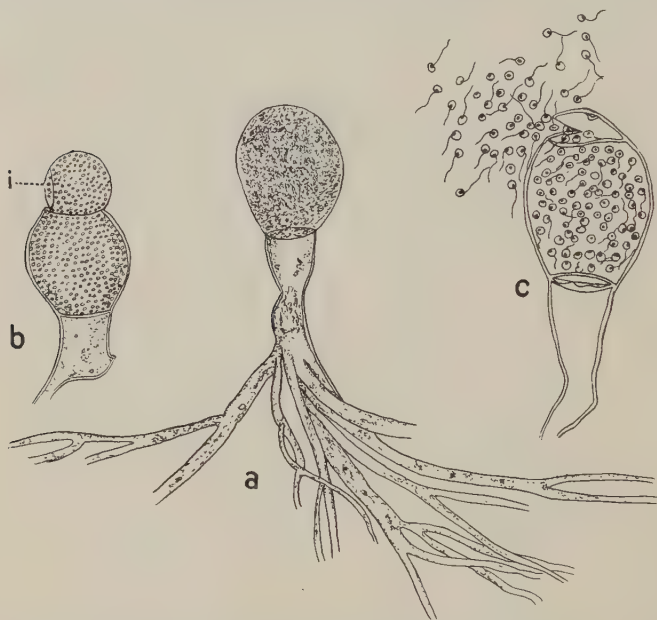
Fig. 24. *Macrochytrium botrydioides* von Minden; *a*, mature plant, with sporangium; *b*, emergence of vesicle from the sporangium, i, lid; *c*, escape of the zoospores; after von Minden.

swell (fig. 23 *b*, *c*), and divide to form large parenchymatous masses, the marginal cells of which become spherical and thick walled (fig. 23 *d*); they receive the contents of the remaining cells, and a group of resting spores (fig. 23 *e*) is formed.

HYPHOCHYTRIACEAE

The mycelium of the Hyphochytriaceae is coarse and shows indications of differentiation into a basal and an apical region.

[1] Butler, 1907.

Macrochytrium botrydioides[1] grows on rotten fruit in foul water. The germinating zoospore forms a relatively massive main axis, attached to the substratum by a well-developed system of rhizoids; it bears a single lateral branch, from the end of which a globose sporangium is cut off (fig. 24 *a*). When the sporangium is mature, a lid forms in the outer layer of the wall (fig. 24 *b*), the contents emerge, surrounded by a delicate membrane, and the zoospores escape (fig. 24 *c*), when the latter bursts.

The habit of *Macrochytrium* recalls, on one side, that of the Rhizidiaceae, and, on the other, that of the Leptomitaceae; the zoospores (fig. 24 *c*) have the characters usual in the Chytridiaceae, and the manner of dehiscence of the sporangium is reminiscent of *Cladochytrium*. The genus may be regarded as a link between the Archimycetes and the Saprolegniales.

ANCYLISTALES

In the Ancylistales the thallus is a simple or branched filament, relatively wide in proportion to its length. At maturity the thallus is divided into a chain of segments, each of which functions as an organ of reproduction. The oogonium contains a single oospore; periplasm has not been recognised.

There are few species, all included in one family.

ANCYLISTACEAE

The members of the Ancylistaceae attack Conjugatae.

The zoospore of *Lagenidium Rabenhorstii*[2] (fig. 25 *a*) is reniform, with two laterally inserted cilia; it comes to rest on a filament of *Spirogyra*, and enters by means of a germ tube. Within the host, a swelling forms at the tip of the germ tube, the contents of the zoospore pass into the enlargement, from which one or more filaments arise, and by apical growth give origin to the thick, short, simple or branched tubes of the mycelium (fig. 25 *b*). The parasite is confined to one host cell, and the extent to which it is developed is influenced by the presence of other parasites in the same cell. During the period of growth, the thallus is aseptate, but, when growth ceases, transverse walls are laid down at irregular intervals, and divide the whole into a number of segments which may be-

[1] von Minden, 1916.   [2] Zopf, 1884; Atkinson, 1909 i.

come zoosporangia, or may be converted into sexual organs. The sporangia bear long exit tubes projecting into the water outside the host (fig. 25 b); as in *Pythium*, the partly differentiated contents of the sporangium pass into a vesicle at the end of the tube, and the formation of the zoospores is completed there (fig. 25 c).

As a rule, a cell of the host contains more than one individual of *Lagenidium*; antheridia and oogonia may occur in the same thallus, but the dioecious condition is also realised. The antheridium puts out a conjugation tube, and unites with an oogonium; the contents of the former pass into the latter, remain distinct for
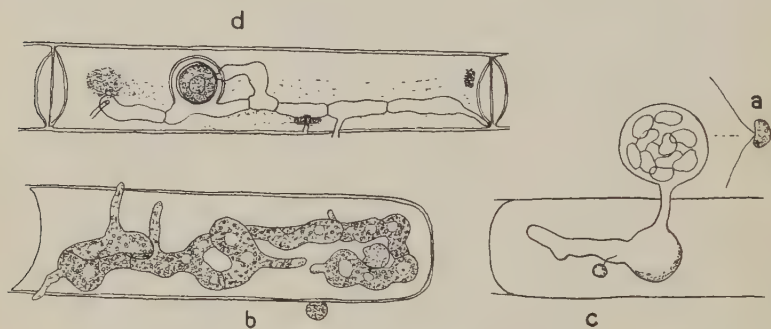
Fig. 25. *Lagenidium Rabenhorstii* Zopf; a, zoospore, × 720; b, thallus within the host, × 540; c, small plant with zoospores in the vesicle, × 720; d, monoecious plant, with an empty antheridium and an oospore, × 720; after Zopf.

a short time, and then fuse; the mature oospore has a two-layered, smooth, colourless wall, and contains a single nucleus (fig. 25 d).

In *Myzocytium proliferum*[1] the vegetative thallus is divided by a number of deep constrictions and, later, by septa. The zoosporangia and sexual organs develop as in *Lagenidium*, but the zoospores are nearly mature when they pass into the vesicle, and the monoecious condition is commonly encountered. In neither genus are oospheres formed before fertilisation; contraction of the contents of the oogonium takes place whilst fertilisation is in progress. Starved specimens may consist of a single sporangium, and can only be distinguished from *Olpidium* at the time of the emergence of the zoospores.

[1] Zopf, 1884.

Protascus subuliformis[1] occurs as a stout cylindrical filament in the bodies of eelworms; septa form (fig. 27 *a*), and the thallus breaks up into a few multinucleate segments. These increase in size, their nuclei divide, and each segment is converted into a sporangium from which non-motile club-shaped spores (fig. 27 *b*) are expelled from an exit canal which passes through the skin of the host (fig. 27 *c*). As eelworms occur together in large numbers, the spores readily come in contact with a new host.
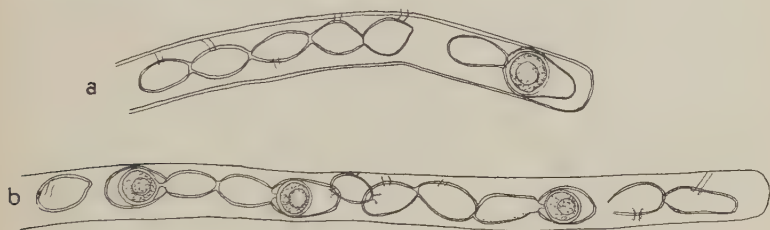
Fig. 26. *Myzocytium proliferum* Zopf; *a*, two plants in *Mesocarpus*, one consists of an antheridium and an oogonium, the other of five sporangia; *b*, large plant bearing sporangia and sexual organs; both × 430; after Zopf.
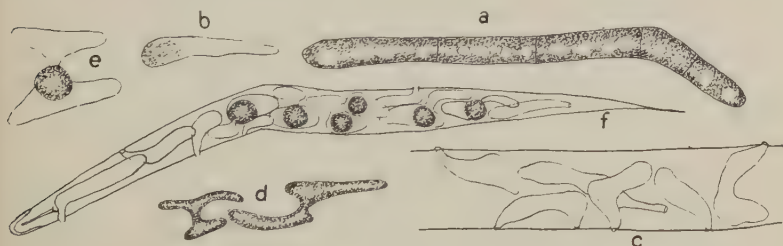
Fig. 27. *Protascus subuliformis* Dang.; *a*, vegetative filament, × 1075; *b*, a spore, × 1460; *c*, empty sporangia within host, × 640; *d*, conjugation, × 270; *e*, oospore, × 385; *f*, eelworm containing oospores and empty sporangia, × 270; after Maupas.

Sometimes, however, after the thallus has broken up, two segments of unequal size, probably derived from different thalli, put out papillae (fig. 27 *d*) towards one another; their contents shrink, a pore opens in the united tips of the papillae, and the contents of the smaller segment pass slowly into the larger. Fusion occurs, and the united contents form a spherical oospore, surrounded by a thick wall of cellulose (fig. 27 *e*).

[1] Maupas, 1915.

In *Protascus* there seems to be a distinct relation between the production of non-motile spores and the gregarious habits of the host; this relationship is even more striking in *Ancylistes*, also a parasite of organisms which live in large colonies. *Ancylistes Closteri*[1] attacks *Closterium*. In early stages the parasite consists of a rather thick, simple or branched filament, which at maturity is divided by septa into a number of segments, each equivalent to a sporangium. Zoospores are not formed, but the contents of each segment pass into a tubular outgrowth, and move forward as it elongates (fig. 28 *a*); empty portions are cut off by septa. A new host is reached and gripped by a curvature of the tube, and the contents enter through a small pore.

Sexual organs are formed as in *Lagenidium* and *Myzocytium*, and the dioecious condition is usual; antheridia are often formed in thin individuals, oogonia in stout ones. The contents of the antheridium pass into the oogonium through a conjugation tube (fig. 28 *b*), or, if the organs are already in contact, by means of a simple pore. An oospore with a wall of two layers (fig. 28 *c*) is formed; the endospore is apparently used up during germination, when a long tube is put out (fig. 28 *d*); this tube functions like that protruded by the vegetative thallus.

Fig. 28. *Ancylistes Closteri* Pfitzer; *a*, portion of thallus divided into segments which bear infection tubes; *b*, conjugation; *c*, oospore with wall of two layers; *d*, germinating oospore; all × 435; after Dangeard.

Mitochytridium ramosum[2] is a species of doubtful position; it occurs in *Docidium*, but not in other desmids. The thallus is stout and resembles that of *Ancylistes*, but tufts of rhizoids appear here

[1] Dangeard, 1886; Petersen, 1910.   [2] Dangeard, 1911.

and there upon it, and, at maturity, the thallus is converted without septation into a single sporangium (fig. 29); the zoospores are uniciliate.

Fig. 29. *Mitochytridium ramosum* Dang.; mature sporangium; after Dangeard.

PROTOMYCETALES

The Protomycetales include but few species, all parasites in flowering plants. The branching septate mycelium inhabits the intercellular spaces of the host; haustoria are not formed. Intercalary or terminal resting sporangia develop within the substratum, and afterwards give rise to non-motile spores which have a tendency to fuse in pairs.

There is one family, the Protomycetaceae.

PROTOMYCETACEAE

Protomyces macrosporus[1] causes elongated swellings on the stems and veins of the leaves of *Aegopodium Podagraria* and other Umbelliferae. Spores come to rest on the surface of the host, insert germ tubes between the epidermal cells, and give rise to a septate mycelium, the segments of which are multinucleate. After a time, certain of the segments receive the contents of their neighbours, swell up, and develop a wall of three layers. The rounded resting sporangium so formed remains quiescent during the winter; in spring, the outer layers of the wall split, and the contents emerge in a sac formed by the expanded inner layer of the wall (fig. 30 *a*). The increase in size of a centrally placed vacuole forces the cytoplasm into a peripheral layer which is cut into uninucleate portions by radially directed furrows. Nuclear divisions follow, and each portion is converted into four spores, which first lie in the peripheral layer, and later form a ball at the apex of the rounded sporangium. The wall splits, the ball of spores is expelled with some violence, and the elongated ellipsoid spores scatter a

[1] von Büren, 1915, 1922.

little, put out short processes, and fuse in pairs. Infection of the host follows, and a new life cycle is begun. In *Protomyces pachydermus*[1], there is the same sequence of events (fig. 30 *b*, *c*), but the sporangial sac is elongated.

Protomyces inundatus[2] attacks *Apium inundatum*; it gives rise to sporangia which require a period of rest, and to others which liberate spores forthwith; they may be formed within the resting sporangium, or within an outgrowth from it. In *Taphridium umbelliferarum*[2], the spores are formed within the resting sporangium,
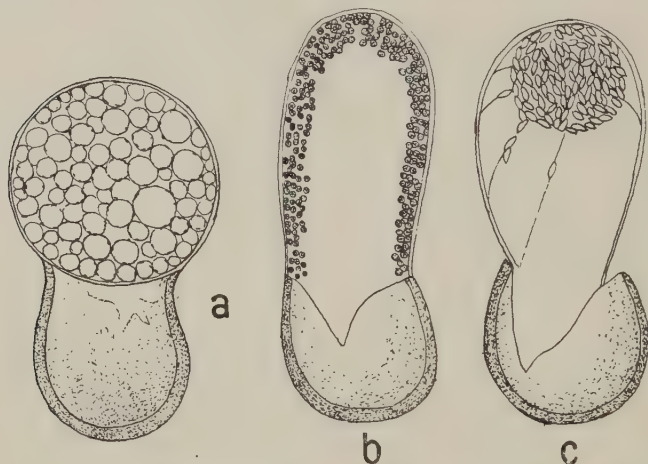
Fig. 30. *Protomyces macrosporus* Unger; *a*, emergence of sporangial sac. *Protomyces pachydermus* Thümen; *b*, spores lying in a peripheral layer; *c*, spores grouped in a ball at the apex of the sac; all × 340; after von Büren.

but they are frequently set free from a thin-walled sac which develops as they mature, and in *Taphridium algeriense*[2] it appears that the spores are cut out from a peripheral layer in the resting sporangium, from which they are set free without the formation of a sac. In this species, although the mycelium ramifies widely in the host tissue, the thin-walled resting sporangia are formed only beneath the epidermis.

The nuclei of the Protomycetaceae are small, and nuclear details are scanty. There is evidence[1] that the spores which fuse are uninucleate, and that nuclear fusion follows spore fusion; sugges-

[1] von Büren, 1915, 1922.   [2] Juel, 1921; von Büren, 1922.

tions have been made that a reducing division precedes the forma-
tion of the spores, but the small nuclei render this difficult to
demonstrate.

The position of the Protomycetales is doubtful. The spores are
formed by a process of cleavage very like that in other Phyco-
mycetes, and the tendency of the spores to fuse in pairs may be
of some moment, recalling the isogamy in *Synchytrium* and *Olpi-
dium*; alternatively, however, this fusion may prove to be a case
of pseudapogamy. On the whole, it seems best, as a provisional
measure, to place the alliance in the Archimycetes, with which they
seem to be most nearly connected.

OOMYCETES

The Oomycetes contain about 200 species; many live as para-
sites or saprophytes in water, others inhabit the intercellular spaces
of Phanerogams, and a few are saprophytes in the soil. They are
distinguished by the possession of a well-developed mycelium and
by the method of sexual reproduction, involving the co-operation
of an antheridium and oogonium.

It may be said broadly that the lower members of the group are
aquatic, the higher terrestrial. In the aquatic species the sporangia
liberate zoospores; in amphibious species zoospores are set free
when abundant moisture is present, but, under relatively dry con-
ditions, the sporangium often puts out a germ tube and functions
as a conidium. In *Pythium ultimum*[1], a saprophyte in the soil, and
in the species of *Peronospora*, this is invariably the case. With the
emphasis of the conidial habit there is a general tendency for the
sporangia to mature in groups, whereas the production of spor-
angia in succession upon the same branch system characterises the
aquatic and amphibious species. Renewal of the sporangium by
proliferation occurs chiefly in aquatic forms; the development of
sporangia in basipetal chains, or on sympodial branch systems, is
found in aquatic and terrestrial species.

With the exception of *Monoblepharis*, in which spermatozoids
occur, the contents of the antheridium pass through a conjugation
tube into the oogonium. The latter contains one or more oospheres

[1] Trow, 1901.

in the Saprolegniaceae, a solitary oosphere in all other families.
In the Saprolegniaceae the oospheres are formed from the contents
of the oogonium by a process of cleavage[1]; furrows pass out from
a central vacuole, and delimit uninucleate masses; all the contents
are used up in this way. In the Monoblepharidaceae the uninu-
cleate contents of the oogonium shrink somewhat, and a single
oosphere is formed; it is not clear if any material remains unused[2].
In other Oomycetes, the single oosphere lies free in the oogonium,
surrounded by some residual material, the **periplasm**, which
assists in the formation of the wall of the oospore, after fertilisation
has occurred. The antheridium may be **androgynous**, that is,
formed in the stalk of the oogonium, or in a branch arising from it;
or it may be **diclinous**, when it develops in a branch arising
independently of that bearing the oogonium. In most cases, the
antheridium is applied to the side of the oogonium, and is then
paragynous, but in *Trachysphaera*[3] and in most species of *Phyto-
phthora* the developing oogonium grows through the antheridial
branch, so that the antheridium surrounds the base of the oogonium,
and is **amphigynous**[4].

The aquatic Oomycetes are particularly sensitive to the environ-
ment, in respect to the formation and behaviour of their repro-
ductive organs. In their usual habitats, the species of *Sapro-
legnia* vary and in culture[5] their behaviour may be profoundly
modified by the composition of the medium. *Saprolegnia mixta*[6],
grown with plentiful supplies of carbohydrate, and frequently
transferred to fresh solutions, has been maintained in a purely
vegetative condition for six years, though portions of the mycelium
yielded reproductive organs soon after they had been transferred
to pure water. *Saprolegnia hypogyna*[7] seldom forms antheridia on
dead insects, but readily gives them in solutions containing haemo-
globin in conjunction with inorganic phosphates, nitrates and salts
of potassium; indeed, under such conditions, it appears that the
material of young oospheres is diverted to the formation of
antheridia. It is probable that the reproductive organs tend to
form in solutions which are nearly but not quite exhausted of

[1] Claussen, 1908.
[2] Thaxter, 1895 i.
[3] Tabor and Bunting, 1923.
[4] Murphy, 1918.
[5] Kauffman, 1908; Coker, 1923.
[6] Klebs, 1899.
[7] Kauffman, 1908.

their nutritive material[1], and at the expense of substances stored in the hyphae. Suitable treatment leads to the development in *Saprolegnia*[2] of characters which, when they occur in nature, are used to separate genera. A comparison may be made with the behaviour of *Pythium*[3] in relation to the substratum, and with the manner of development of the sporangia of *Phytophthora*[4] and of the Peronosporaceae[5], according to external influences.

The Oomycetes are divided into the following alliances:

Habitat aquatic	
Spermatozoids present	MONOBLEPHARIDALES
Spermatozoids absent	SAPROLEGNIALES
Habitat subterranean, subaerial or endophytic	PERONOSPORALES

MONOBLEPHARIDALES

The Monoblepharidales are characterised by the union of a motile male gamete with an oosphere contained in an oogonium. There is one family, the Monoblepharidaceae, with about six rare species, all saprophytes on vegetable material in water; they appear to the naked eye as small, whitish or yellowish tufts.

MONOBLEPHARIDACEAE

The best-known species of the Monoblepharidaceae is *Monoblepharis sphaerica*[6] (fig. 31). The plant is attached to the substratum by delicate rhizoids; thin, stiff branches stand out in the water. Older portions of hyphae show foamy contents. In the formation of the cylindrical zoosporangium, cytoplasm and nuclei accumulate in the end of a branch, and a septum forms below; a zoospore is organised around each nucleus present. Owing to the narrow space, the zoospores usually lie in a row; they escape from the apex of the sporangium. Before the terminal sporangium discharges, a second is formed immediately below it; by repetitions of the process basipetal chains of sporangia come into being.

The zoospores are monoplanetic and uniciliate; in appearance and gait they resemble those of many Chytridiales. They swim for a time, settle on a suitable substratum in well-aerated water,

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[1] Obel, 1910.
[2] Lechmere, 1910, 1911; Collins, 1920.　　　　　[3] Cf. p. 94.
[4] Cf. p. 40.　　　　　[5] Cf. pp. 93, 105.
[6] Cornu, 1872; de Lagerheim, 1900; Woronin, 1904.

and usually put out two germ tubes, one of which gives rise to the system of rhizoids, the other to the fertile hyphae.

The oogonium appears as a terminal enlargement; an antheridium is usually organised immediately beneath, and ordinarily shows no swelling. By the sympodial branching of the fertile hyphae groups of paired sexual organs may be formed.

In the formation of the oogonium, a single nucleus and some cytoplasm are cut off in the terminal swelling by a basal septum. Nuclear division does not occur; the contents of the oogonium shrink, water is expelled, and a single oosphere results. The antheridia contain five or six nuclei; each becomes the nucleus of a spermatozoid. A small lateral beak protrudes from the antheridium, and the uniciliate spermatozoids emerge (fig. 31 b); they are smaller than the zoospores, which they otherwise resemble in appearance.

A pore opens in the wall of the mature oogonium, and a substance is extruded which seems to attract the male gametes. They alight on the oogonium (fig. 31 c), where they crawl for a time in amoeboid fashion. Finally, one enters the pore and fuses with the oosphere. After fusion, the zygote may show some
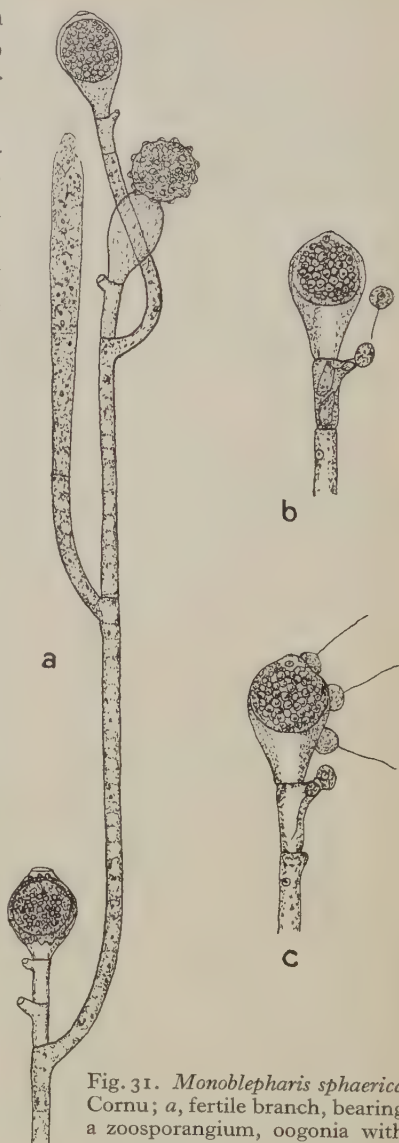
Fig. 31. *Monoblepharis sphaerica* Cornu; a, fertile branch, bearing a zoosporangium, oogonia with oospores, and empty antheridia below them, $\times$ 520; b, emergence of spermatozoids; c, spermatozoids creeping on the oogonium; after Woronin.

motility; it frequently travels to the base of the oogonium, then moves towards the pore, and sometimes passes through it. A thick, warted wall is formed around the oospore (fig. 31 *a*); as it is being laid down, the two nuclei fuse. The germination of the oospore has not been seen in *Monoblepharis sphaerica*, but there is evidence from other species that, after a period of rest, the wall splits and a stout germ tube is produced.

Monoblepharis sphaerica has been found only in Europe; an American species, *Monoblepharis fasciculata*[1], differs from it in certain important respects. In this species, the zoosporangium is swollen, and liberates biciliate zoospores. The antheridium is terminal, with an oogonium immediately below it; groups of sexual organs are formed by the branching of the fertile hyphae. The spermatozoids are smaller than the zoospores, and are uniciliate. In *Monoblepharis macrandra*[2] the sporangia are renewed by proliferation.

SAPROLEGNIALES

The Saprolegniales are aquatic fungi, living in fresh or brackish water. The mycelium is usually aseptate and branched; it often shows differentiation into a basal, nutritive region and an apical, fertile region. The zoosporangia do not usually differ greatly in appearance from the tips of the hyphae, and, when several occur together, they arise in succession. There is little indication within the alliance of a tendency to the production of definite sporangiophores.

Uniciliate and biciliate zoospores occur; the latter often show diplanetism. There is some evidence[3] that the species with uniciliate zoospores contain little or no cellulose in the walls of the hyphae, and that cellulose walls and biciliate zoospores go together.

Oogonia and antheridia arise at the ends of hyphae; the entire contents of the oogonium are transformed into one or more oospheres. Fertilisation is brought about by means of a conjugation tube, formed after the antheridium and oogonium have come into contact. Although pits often occur in the wall of the oogonium, it does not necessarily follow that the conjugation tube enters through one of them.

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[1] Thaxter, 1895 i. [2] Woronin, 1904.
[3] Petersen, 1910; Butler, 1911; von Minden, 1916.

The Saprolegniales may be divided as follows:

Hyphae not constricted	SAPROLEGNIACEAE
Hyphae constricted at intervals, or at their base	LEPTOMITACEAE

SAPROLEGNIACEAE

The Saprolegniaceae include about one hundred species, growing as saprophytes or parasites in water, or in wet soil[1]. With few exceptions the mycelium is continuous in the vegetative condition; constrictions do not occur in the course of the hyphae or at the insertion of branches. Freely branched vegetative hyphae creeping on or in the substratum and bearing rhizoidal filaments may be distinguished from the rather stouter fertile branches immersed in the surrounding water. Chlamydospores may be formed by the development of septa in the hyphae, and in this family are often known as gemmae; they occur in several species of *Saprolegnia*, and are particularly abundant in *Saprolegnia torulosa*.

In the development of the primary zoosporangia, an accumulation of cytoplasm and nuclei at the end of a fertile hypha is cut off by a wall; the sporangium is cylindrical or club-shaped in most species; it is globose in *Pythiopsis cymosa*, and irregular in *Jaraia salicis*[2]. Secondary sporangia are formed by proliferation in *Saprolegnia*[3] (fig. 32 a);

Fig. 32. *Saprolegnia monoica* Prings.; *a*, renewal of the sporangium by proliferation of the fertile hypha, × 225; after Coker. *Achlya racemosa* Hildebr.; *b*, sympodium of sporangia and formation of groups of cysts, × 55; after Pringsheim. *Dictyuchus* sp.; *c*, two successively formed sporangia, the upper showing crowded empty cysts, × 225; after Weston.

in *Achlya*[3] (fig. 32 b) they arise in lateral branches borne at the base of the immediately preceding sporangium; in *Dictyuchus*[3] (fig. 32 c) chains of sporangia are formed in basipetal succession.

[1] Harvey, 1925.   [2] Nemec, 1913 ii.   [3] de Bary, 1881 i, 1888.

Zoospores are differentiated by a process of cleavage[1]. A centrally placed vacuole in the young sporangium pushes the cytoplasm and nuclei against the wall; furrows appear on the inner face of this peripheral layer and spread radially outwards, so that several uninucleate rudiments are cut out; the rudiments contract somewhat, water is expelled from the sporangium, and shrinkage occurs. As a result, the initials of the zoospores are crowded together, and their outlines are difficult to determine. The final differentiation is completed by further shrinkage of the rudiments; they round off, and are now ready to escape. Nuclear
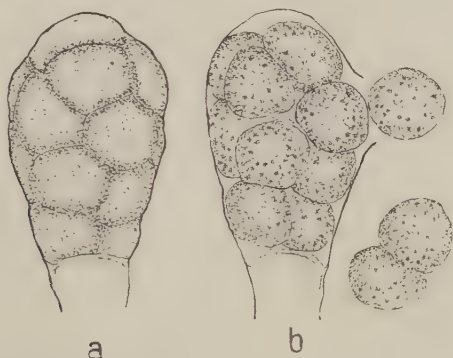
Fig. 33. *Thraustotheca clavata* (de Bary) Humphrey; *a*, mature sporangium; *b*, escape of sporangiospores; × 1120; after Weston.

divisions do not occur in the formation of the zoospores; the process is in agreement with the manner of delimitation of asexual spores throughout the Phycomycetes.

Diplanetism[2] is well shown by the zoospores of *Saprolegnia* and of *Leptolegnia*. In these genera pyriform zoospores with two apical cilia escape from the sporangium; encystment follows a short period of activity, and, after a rest of about twenty-four hours, each cyst gives rise to a zoospore shaped like a coffee bean, with two laterally inserted cilia. If contact is made with a suitable substratum, the zoospore produces a germ tube. In *Achlya*[3] and *Aphanomyces*[3], it is possible that pyriform zoospores are formed within the sporangium; zoospores may be seen there moving by means of cilia, but free-swimming pyriform zoospores have not

[1] Schwarze, 1922.
[2] Leitgeb, 1869; Butler, 1907; Atkinson, 1909 ii; Weston, 1919.
[3] Coker, 1923.

been observed in the water outside. The zoospores emerge and encyst at the mouth of the sporangium, forming a ball of cysts (fig. 32 *b*), from which zoospores with two laterally placed cilia are afterwards set free. The suppression of the first motile stage is carried still further in *Thraustotheca*[1] (fig. 33), in which the cysts escape through rents in the wall of the sporangium. In *Dictyuchus*[2] the cysts remain within the sporangium, where they give the appearance of a network of cells, and each zoospore escapes separately through a pore in the wall (fig. 32 *c*); they bear two lateral cilia.
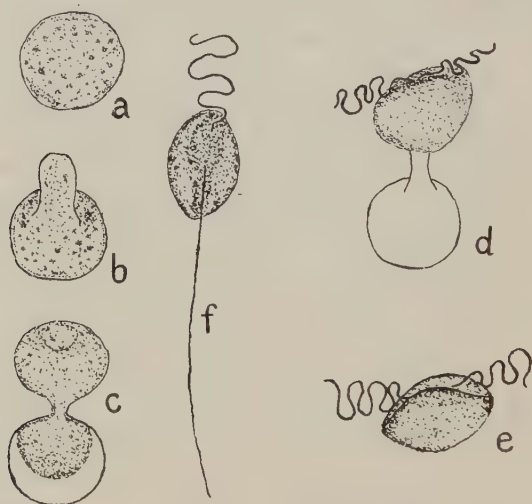
Fig. 34. *Dictyuchus* sp.; *a*, cyst; *b*, *c*, *d*, stages in emergence of the zoospore from the cyst; *e*, *f*, two views of the zoospore; all × 1400; after Weston.

These zoospores may encyst again, after they have emerged from the sporangium; the cysts give rise to zoospores of the same type (fig. 34). Finally, in *Aplanes*[3] motile spores are rarely seen; the spore initials germinate *in situ* and protrude germ tubes through the wall of the sporangium.

Pythiopsis cymosa[4] has pyriform zoospores with two apical cilia, resembling the first type in *Saprolegnia*; they swim for a time and then germinate; zoospores with laterally inserted cilia are not known in this species.

[1] Weston, 1918. [2] Weston, 1919.
[3] Coker, 1923. [4] de Bary, 1888.

Antheridia and oogonia develop as vegetative activity decreases. Normal fertilisation occurs in *Saprolegnia monoica*[1], *Achlya polyandra*[2], *Achlya americana*[3], *Aphanomyces laevis*[4], in dioecious species of *Dictyuchus*[5] and in other forms; in still others, although antheridia may be produced, parthenogenesis occurs. The antheridia are club-shaped, and often bent; they usually arise terminally on special branches. In *Saprolegnia hypogyna*[6], however, they are androgynous in the stalk of the oogonium, and in *Saprolegnia monoica*[7] they are androgynous in a branch, whilst *Saprolegnia diclina*[8] shows the diclinous condition. The antheridial branch is often long, and may branch and bear several terminal antheridia.
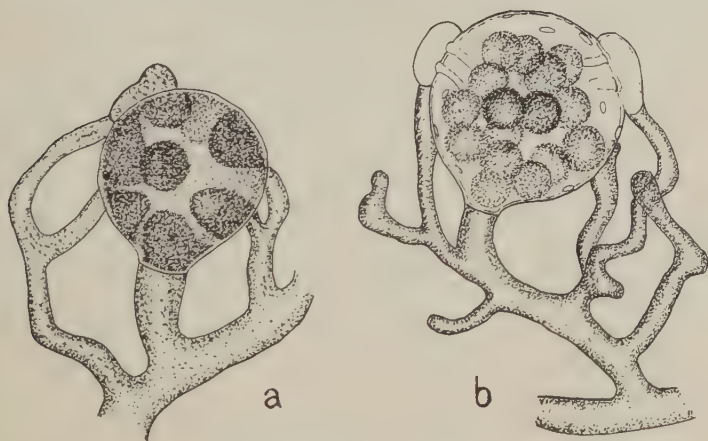
Fig. 35. *Saprolegnia monoica* Prings.; *a*, oogonium with oospheres in course of formation; *b*, oogonium at time of fertilisation, with conjugation tubes entering from the antheridia; × 280; after Pringsheim.

In *Saprolegnia monoica*[1] the young oogonium contains many nuclei and much cytoplasm; a central vacuole develops, and, as it enlarges, degeneration of some of the contents of the oogonium occurs. Finally, the cytoplasm and nuclei form a rather thin peripheral layer; here the nuclei divide, many of the daughter nuclei degenerate, and the survivors are enclosed in a number of uninucleate oospheres derived from the contents of the oogonium by a process of cleavage (fig. 35 *a*); periplasm cannot be recognised.

[1] Claussen, 1908.　[2] Mücke, 1908.　[3] Trow, 1899, 1905; Davis, 1903, 1905.
[4] Kasanowsky, 1911.　　　　[5] Couch, 1926.　　　　[6] de Bary, 1888.
[7] Pringsheim, 1858.　　　　[8] Coker, 1923.

The antheridium contains a few nuclei; these divide at the same time as those of the oogonium. Simple or branched conjugation tubes enter the oogonium (fig. 35 *b*), and one male nucleus passes to each oosphere. Eventually the male and female nuclei fuse, and, though confirmation is required, it is probable that the reducing division takes place at the germination of the oospore.

The wall of the ripe oospore is smooth and colourless, rather thick, and somewhat refractive. A thick epispore and a thinner endospore can generally be distinguished. The contents are often brown or yellow, owing to the accumulation of fatty matter, and the ripe oospore contains a large oil drop, the centric or excentric position of which is of systematic importance. The germination of the oospore may occur soon after maturity, or it may be preceded by a lengthy resting period. As a rule, a single germ tube is produced, bearing one or more sporangia. In *Aphanomyces euteiches*[1], the cause of root rot in peas, and one of the few members of the family which does not live in water, the oospores germinate without a rest; when placed in a nutrient solution they give rise to germ tubes, but in water they liberate zoospores.

Zoophagus insidians[2] and *Sommerstorffia spinosa*[3] live among filamentous algae in fresh water; short branches from the mycelium become attached to living rotifers, which are then entered by the fungus, and their contents digested.

Leptomitaceae

The Leptomitaceae include about a dozen species; they are saprophytes, often found in heavily contaminated water. The hyphae show constrictions, either at intervals along their length or at the point of insertion on the parent hypha; similar constrictions occur below the organs of reproduction. Cellulin, a refractive substance probably related to cellulose, is abundant in the Leptomitaceae, either in the thickenings at the constricted points or as loose granules in the hyphae. Zoosporangia are formed terminally in the branches. In *Rhipidium*, *Araiospora* and *Sapromyces*, antheridia and oogonia are also developed at the ends of branches; a single oosphere is formed, and periplasm is present. In *Apodachlya*, *Blastocladia* and *Allomyces* resting structures which may be modified

[1] Jones and Dreschler, 1925.
[2] Sommerstorff, 1911; Mirande, 1920.   [3] Arnaudow, 1923.

Fig. 36. *Rhipidium americanum* Thaxter; *a*, mature plant bearing sporangia, × 50; *b*, contents of sporangium emerging in a vesicle, × 160; *c*, rupture of vesicle and escape of the zoospores, × 160; *d*, mature oospore in oogonium, with attached antheridium, × 320; all after Thaxter.

oogonia are found, but fertilisation has not been demonstrated. Sexual organs are unknown in *Leptomitus*.

Fig. 37. *Araiospora pulchra* Thaxter; *a*, habit of plant with sexual organs, × 50; *b*, spinose and smooth sporangia, × 100; *c*, antheridium and oogonium, × 400; after Thaxter.

Fig. 38. *Sapromyces Reinschii* Fritsch; portion of plant, bearing sporangia, × 120; after Pringsheim.

The thallus of *Rhipidium americanum*[1] (fig. 36 *a*) resembles a pollarded tree, with a stout main axis derived from the body of the

[1] Thaxter, 1896 iii; von Minden, 1916.
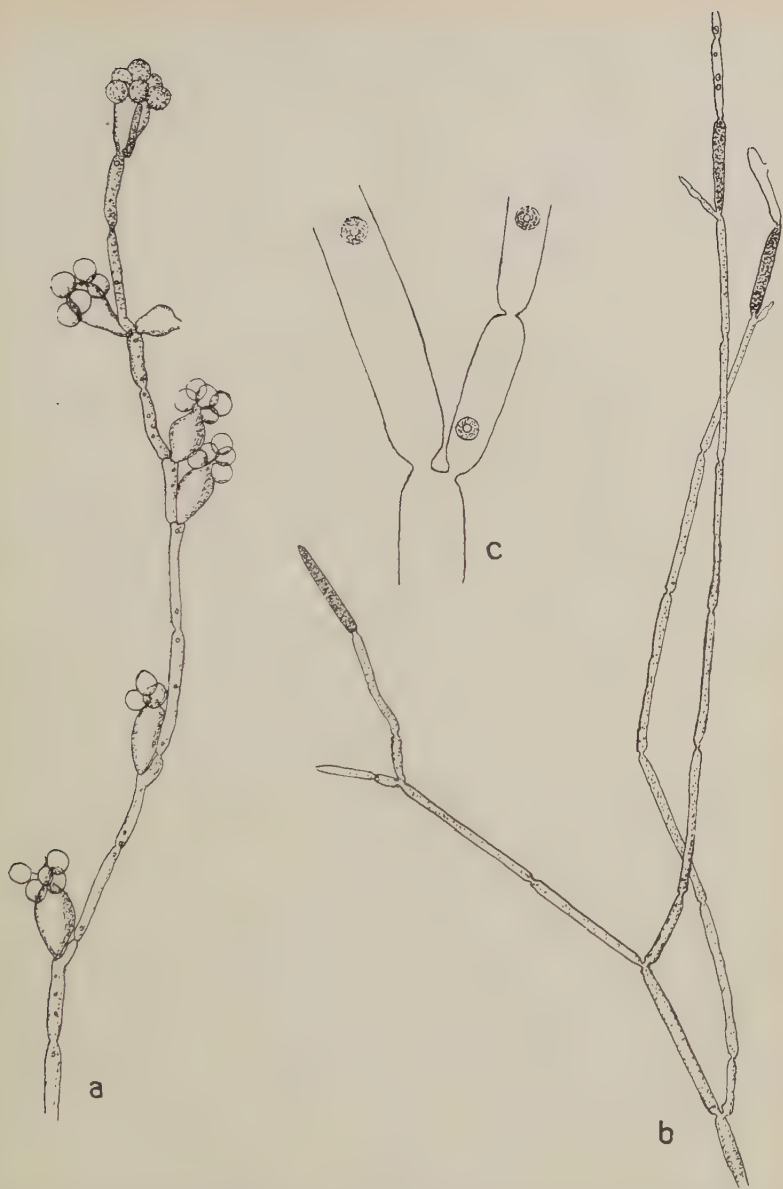
Fig. 39. *Apodachlya pyrifera* Zopf; *a*, portion of plant bearing sporangia, and showing groups of encysted zoospores, × 250; after Zopf. *Leptomitus lacteus* Ag.; *b*, portion of mycelium, with sporangia, × 100; *c*, small portion of mycelium showing constrictions and cellulin granules, × 300; after Pringsheim.

zoospore, a basal system of rhizoids, and an apical group of branches on which secondary branches are borne; these carry the reproductive organs. The zoosporangia are developed in succession in sympodia; they are of two types. From one, spores are liberated immediately; the other type is capable of a period of rest. At the time of the escape of the zoospores a lid formed from the wall at the apex of the sporangium is lifted up (fig. 36 *b*), and the spores

Fig. 40. *Blastocladia Pringsheimii* Reinsch; a plant bearing sporangia; after Thaxter.

emerge in an elongated vesicle, formed from the inner layer of the wall; it bursts and sets free the biciliate zoospores (fig. 36 *c*). The oogonia are terminal and spherical; the antheridia appear as small terminal segments of lateral branches; these are long and sinuous and wind about among the other branches as they find their way to the oogonia. A conjugation tube permits the transfer of material from the antheridium to the oogonium (fig. 36 *d*).

Araiospora pulchra[1] (fig. 37) resembles *Rhipidium* in most re-

[1] King, 1903.

spects; the resting sporangia are beset with spines. *Sapromyces Reinschii*[1] (fig. 38) shows a decline of the arborescent habit; this is still more pronounced in *Apodachlya pyrifera*[2] (fig. 39 *a*); in this species it is possible to distinguish main hyphae with thinner lateral branches, but there is no regular form to the thallus. Zoosporangia appear as swollen terminal segments of the branches;

Fig. 41. *Allomyces arbuscula* Butler; plant with sporangia, and a few resting spores; after Butler.

the zoospores emerge as in *Achlya*, encyst in a group at the mouth of the sporangium, and finally escape with two lateral cilia. The sporangia are renewed by sympodial branching of the fertile hyphae.

In *Leptomitus lacteus*[3] (fig. 39 *b*), a species found in streams contaminated with sewage, the mycelium consists of copiously branched hyphae with no indications of a main axis. The hyphae

[1] Reinsch, 1878; Thaxter, 1896 iii.   [2] Zopf, 1888.
[3] Pringsheim, 1858; Guilliermond, 1922; Coker, 1923.

are deeply constricted, but pores allow of communication be-
tween the segments (fig. 39 c), in each of which a granule of cellulin
is a conspicuous object. The sporangium is formed in the un-
differentiated terminal segment of a filament; a granule of cellulin
lodges in the pore, and the zoospores are cut out by a process of cleavage. They are set free as pyriform structures with two apical cilia. As the sporangium empties another is organised in the segment next below, so that chains of these organs may be found.

The tree-like form cha-
racteristic of *Rhipidium* is encountered in *Blastocladia Pringsheimii*[1] (fig. 40), a species of obscure affinities, which seems to be connected with the Leptomitaceae by *Allomyces arbuscula*[2] (fig. 41); in *Allomyces* the dichotom-
ously branched thallus is septate from an early stage of development. A sexual process has not been observed in these species; they produce resting structures, which have pitted walls and may be modi-
fied oogonia. The zoospores are uniciliate, as they are also in *Gonapodya siliquaeformis*[3]

Fig. 42. *Gonapodya siliquaeformis* (Reinsch) Thaxter; portion of plant, showing con-
strictions, and renewal of the sporangia by proliferation; after Thaxter.

(fig. 42). This species shows something of the arborescent habit,
with deep constrictions in the hyphae comparable with those of
Leptomitus, and foamy contents recalling those of old hyphae of
Monoblepharis.

[1] Thaxter, 1896 ii.
[2] Butler, 1911; Barrett, 1912 ii; Coker, 1923.
[3] Thaxter, 1895 ii; Petersen, 1910; von Minden, 1916.

PERONOSPORALES

Most of the 200 species of the Peronosporales are intracellular parasites in land plants. The mycelium is richly branched and bears haustoria. Asexual reproduction is by means of zoospores formed in zoosporangia; in many species the same structure may function as a zoosporangium or as a conidium according to external conditions; low temperature and moisture favour the liberation of zoospores, higher temperatures and relative dryness promote direct germination. In most species the sporangiophores emerge from the host plant, while antheridia and oogonia are formed within its tissues; the oogonium contains a single oospore.

There are three families, which may be distinguished as follows:

Species able to live as parasites or as saprophytes; sporangiophores differing little from vegetative hyphae — PYTHIACEAE

Species living as parasites
Sporangia formed in chains on club-shaped sporangiophores crowded beneath the epidermis of the host — ALBUGINACEAE
Sporangia formed singly at the ends of branched sporangiophores which emerge from the host in early stages of development — PERONOSPORACEAE

PYTHIACEAE

The Pythiaceae are characterised by their saprophytic tendencies, the general absence of well-defined sporangiophores, the development of sporangia in succession upon a sympodially branched system of hyphae, and the capacity of the sporangia to form germ tubes or liberate zoospores while still attached.

Pythium de Baryanum[1] is the cause of damping off of seedlings; these are attacked at ground level, the tissues are softened and the seedling falls over. The disease is favoured by excessive moisture, crowding and insufficient ventilation. *P. de Baryanum* grows readily on animal and vegetable material floating in water[2]; under these conditions a well-developed mycelium is formed outside the substratum.

The mycelium is composed of branched hyphae with thicker main strands and thinner lateral branches; the hyphae show an

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[1] de Bary, 1881; Butler, 1907, 1913.   [2] Butler, 1913.

even tapering towards the ends, in this respect recalling the hyphae of the higher Chytridiales. Septa develop in old mycelia within the host; they are abundant in aquatic mycelia on which reproductive organs are in course of formation.

Spherical zoosporangia form terminally on the hyphae, and in undisturbed cultures on insects lying in shallow water liberate zoospores freely[1]. A lateral process is put out (fig. 43 *a*); its end swells
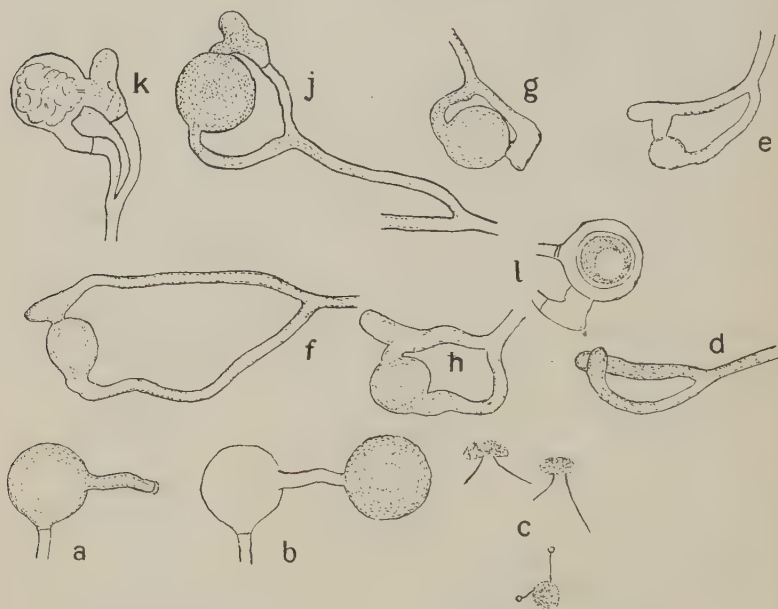
Fig. 43. *Pythium de Baryanum* Hesse; *a*, sporangium with lateral hypha; *b*, formation of the vesicle; *c*, free zoospores, one withdrawing its cilia; *d*, early stage in formation of the sexual organs; *e*,–*k*, successive stages in the development of the sexual organs; *l*, oospore within the oogonium; all × 512; after Butler.

(fig. 43 *b*), the contents of the sporangium undergo changes suggesting that rudiments of zoospores have been formed by a process of cleavage, and migrate into the vesicle at the end of the beak. The zoospores mature in the vesicle, and escape when it ruptures; they are bean-shaped, with two cilia inserted in a lateral depression (fig. 43 *c*). Germination takes place upon suitable substrata by means of a germ tube.

On vegetable substrata sporangia develop freely, but they often

[1] Butler, 1913.

function as conidia[1]; a lateral process grows out, branches, and gives rise to a mycelium.

Sexual organs[1] appear when the host has been killed and the fungus is living as a saprophyte. As a rule, an oogonium arises terminally on a lateral branch, and an antheridium is cut off in a similar position from a branch of the stalk of the oogonium (fig. 43 *d–g*); the tips of the two organs are brought together by curvatures of the hyphae. Sometimes the antheridium is organised in the stalk of the oogonium, immediately below that organ; this recalls the condition in *Monoblepharis sphaerica*. Occasionally the antheridium is formed at the end of a branch arising from the
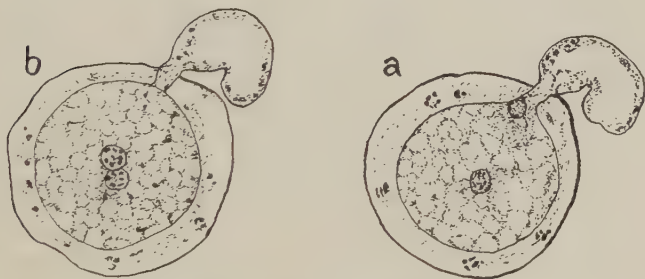
Fig. 44. *Pythium de Baryanum* Hesse; *a*, discharge of contents of the antheridium into the oogonium; *b*, association of the sexual nuclei; both ⨯ 1300; after Miyake.

mycelium independently of the oogonial branch; such an arrangement is comparable with that found in *Saprolegnia diclina*.

At first, both the oogonium and antheridium are multinucleate; septa cut them off from their stalks (fig. 43 *j, k*). As the oogonium ripens its contents contract to form a rounded oosphere; periplasm is scanty. The nuclei pass to the periphery of the ooplasm and divide once; of the daughter nuclei all degenerate but one, this being the functional female nucleus. The nuclei in the antheridium also divide once, and subsequent degeneration reduces their number to one. A receptive papilla forms where the antheridium touches the wall of the oogonium. A conjugation tube passes from the antheridium into the ooplasm, opens, and emits the male nucleus (fig. 44 *a*); some cytoplasm is also transferred, and apparently mingles with the periplasm[2]. The two nuclei come together

[1] Butler, 1913.   [2] Miyake, 1901.

(fig. 44 b) and soon fuse; the oospore forms a thick stratified wall and rests for some months. Germination is effected by the production of a germ tube.

Pythium de Baryanum may be taken as a central type of the genus, other species of which show divergences in important respects. In *Pythium gracile*[1] the sporangia are filamentous and do not differ in appearance from the vegetative hyphae; they are not cut off by septa. The contents of a portion of a hypha are transformed into zoospores, a vesicle forms at the apex of the hypha, and the zoospores emerge in the manner characteristic of the genus. The next portion of the hypha then undergoes the same change, and in this way most of the contents of the mycelium may ultimately escape as zoospores. *Pythium gracile* and other aquatic species attack algae; all produce large crops of zoospores. *Pythium proliferum*[1] (fig. 45 a), also an aquatic species, renews its sporangia by proliferation. So far as is known, the sporangia of the aquatic species never function as conidia; that be-

Fig. 45. *Pythium proliferum* de Bary; a, renewal of the sporangium by proliferation, × 150. *Pythium intermedium* de Bary; b, formation of sporangia in chains, × 300; after Butler.

haviour is characteristic of members of the genus which live in the soil or in higher plants. Although sporangia are in most cases formed singly, in *Pythium intermedium*[1] (fig. 45 b), chains of sporangia are produced; this species may be a link with the Albuginaceae.

The capacity for direct germination possessed by the sporangia seems to be an adaptation to a subaerial habitat where there may not be sufficient water for the successful distribution of zoospores. *Pythium ultimum*[2], a saprophyte occurring in the soil, appears to

[1] Butler, 1907.   [2] Trow, 1901.

be highly specialised in this respect, for its sporangia always behave as conidia.

Throughout the genus, the zoospore, when produced, is bean-shaped with two lateral cilia[1]. In species parasitic in algae it germinates, as in *Lagenidium*, by the passage of the contents into the host cell[2]; in other species a germ tube is developed.

The genus *Phytophthora*[2] is closely allied to *Pythium*, differing mainly in the accentuation of the terrestrial habitat. Flowering plants alone are attacked; the species grow well in artificial culture. The hyphae are wider than in *Pythium*; they live in the intercellular spaces of the host. Irregular septa often appear in old hyphae.

The rather coarse hyphae of *Phytophthora erythroseptica*[3] occur in potato tubers; they are especially abundant at the margin between dead and living tissue. Reproductive organs do not seem to form in the host, but they may be obtained in culture; the fungus grows readily on oatmeal agar. Sporangia are obtained when vigorous mycelium is transferred to sterilised bog water; they develop in succession at the ends of the branches of a sympodial system as pyriform structures; as a rule they give rise to a germ tube, and so behave as conidia.

Antheridia and oogonia arise on short lateral branches, which in early stages of development cannot be distinguished from ordinary vegetative hyphae. They grow towards one another, and the tip of one, the **oogonial incept**, penetrates the other; in the latter dense material accumulates and an antheridium is cut off by one or by two septa. The oogonial incept grows through the antheridium (fig. 46 *a*, *b*); it emerges on the other side and there gives rise to a rounded swelling (fig. 46 *c*) containing cytoplasm and nuclei; this is the young oogonium. Its funnel-shaped base lies within the antheridium, and is cut off from the stalk by a thick irregular plug. Many of the oogonial nuclei disintegrate; the survivors divide once, and, after further disintegration, a single nucleus remains. The contents of the oogonium are now differentiated into a solitary oosphere, surrounded by a little periplasm. The antheridial nuclei also divide once, and then all but

[1] Butler, 1913.
[2] de Bary, 1876; Butler, 1907; Butler and Kulkarni, 1913; Dastur, 1913; Pethybridge, 1913, 1922; Rosenbaum, 1917; Sherbakoff, 1917; McRae, 1918; Fitzpatrick, 1923; Godfrey, 1923; Leonian, 1925.
[3] Pethybridge, 1913; Murphy, 1918.

one break up. Within the antheridium the wall of the oogonium bulges out to form a large receptive papilla; as this is withdrawn a conjugation tube follows and delivers the male nucleus and some cytoplasm into the oosphere; by this time the periplasm has nearly disappeared. A wall is formed around the oospore; the male and female nuclei fuse and the oospore rests (fig. 46 *d*) in a uninucleate condition; its further history is unknown, but in *Phytophthora palmivorum*[1] and other species the oospore gives rise to a short hypha on which sporangia are borne (fig. 47 *a*).
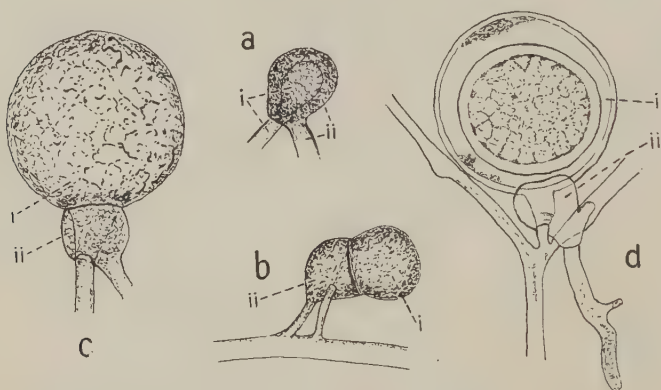
Fig. 46. *Phytophthora erythroseptica* Pethyb.; *a*, penetration of the antheridial branch by the oogonial incept; *b*, emergence of the young oogonium; *c*, later stage in the formation of the oogonium; *d*, ripe oospore, with the empty antheridium attached to the base of the oogonium; i, oogonium; ii, antheridium; all × 860; drawn from living material.

Phytophthora infestans causes a serious disease of potato. It first became notorious in 1845–6, when it caused a potato famine in Ireland, and contributed to the repeal of the Corn Laws. The mycelium is widely distributed in the host; in damp air, sporangia appear in abundance on the leaves, borne on sympodially branched sporangiophores (fig. 47 *b, c*); there is a characteristic swelling beneath each sporangium. Sexual organs do not seem to form in the host, but they have been obtained in culture[2]. They agree in their manner of formation with those of *Phytophthora erythroseptica*, but parthenogenesis also occurs.

[1] Butler, 1907; Fitzpatrick, 1923.
[2] Clinton, 1911; Pethybridge and Murphy, 1913.
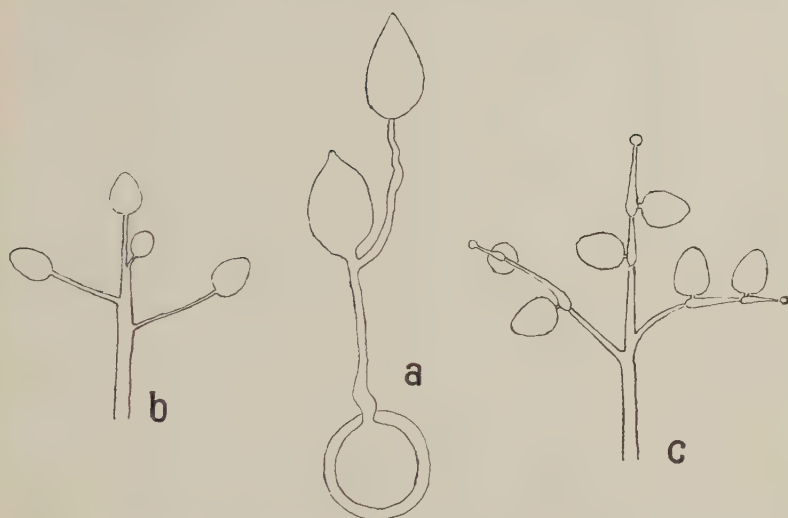
Fig. 47. *Phytophthora palmivorum* (Butl.) Butl.; *a*, germination of oospore, × 400; after Butler. *Phytophthora infestans* de Bary; *b, c*, stages in development of the sporangiophore, × 200; after de Bary.

Fig. 48. *Phytophthora Cactorum* (Lebert and Cohn) Schröt.; *a*, young oogonium; *b, c*, young oogonia and antheridia; *d*, fertilisation; *e, f*, formation of the oospore; all × 500; E. J. Welsford del.

In *Phytophthora Cactorum*[1] (fig. 48) the sexual organs usually develop and function like those of *Pythium de Baryanum*, with a paragynous antheridium, but the antheridium may sometimes be amphigynous. As in *Pythium*, the partly differentiated zoospores may pass into a vesicle before they escape. There is a similar method of discharge in *Phytophthora cryptogea*[2], and in this species the zoosporangia are often renewed by proliferation. A dioecious condition has been described in *Phytophthora Faberi*[3], a tropical species parasitic on cocoa; the emergence of its zoospores is favoured[4] by light, a supply of free oxygen, and a moderate temperature.

Trachysphaera fructigena[5] is also a tropical form, attacking coffee and cocoa. The antheridia are amphigynous, and the oogonia bear numerous, irregular, rounded outgrowths. The sporangia form thick pinkish brown incrustations on the surface of the fruit of the host; in simple cases a single sporangium is borne on the sporangiophore, but usually the latter ends in a swelling on which a whorl of sporangia, or sometimes of secondary fertile branches, is borne. The sporangia are spherical, with many spines projecting from their surface; they are thus quite unlike the sporangia of any other members of the family. They appear to function always as conidia.

Stigeosporium Marattiacearum[6], the fungal constituent in the mycorrhiza of the Marattiaceae, bears some resemblance to *Phytophthora*, and may be a member of the Pythiaceae.

ALBUGINACEAE

The Albuginaceae include some six species, all parasitic in flowering plants. They are characterised by the production of sporangia in chains.

Cystopus candidus[7] attacks *Capsella Bursa pastoris* and other Cruciferae, forming white shining patches on the stems and leaves, and causing deformity of the flowering shoots and fruits. The mycelium consists of rather coarse hyphae which inhabit the intercellular spaces and bear numerous small, rounded haustoria (fig. 49 *a*). Hyphae collect beneath the epidermis; they branch pro-

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[1] Lafferty and Pethybridge, 1922.   [2] Pethybridge and Lafferty, 1919.
[3] Ashby, 1922.   [4] Gadd, 1924.
[5] Tabor and Bunting, 1923.   [6] West, 1917.
[7] *Cystopus candidus* (Pers.) Lév. = *Albugo candida* (Pers.) O. Ktze.

fusely and give rise to a closely packed series of club-shaped sporangiophores, arranged in palisade fashion, perpendicular to the surface of the leaf (fig. 49 *b*, *c*). Dense cytoplasm and five or six nuclei accumulate at the apex of the sporangiophore, a broad septum forms below, and a young sporangium is thus delimited; successive sporangia are cut off in the same way. The septum is

Fig. 49. *Cystopus candidus* (Pers.) Lév.; *a*, portion of mycelium bearing haustoria, ⨯ 400; after de Bary; *b*, group of sporangiophores with chains of sporangia, ⨯ 450; *c*, diagram showing position of sporangiophores beneath the raised epidermis of the host, ⨯ 75.

gelatinous in consistency; it decreases in diameter as the sporangia mature. As the chains of sporangia elongate they press on the epidermis of the host; rupture occurs, the gelatinous links between the sporangia break down under the influence of moisture, and the sporangia are set free. The oldest sporangium develops a thicker wall than its successors; it encounters most resistance from the epidermis. Sometimes in *C. candidus*, and frequently in related species, this sporangium fails to develop further.

In the presence of water, a few biciliate zoospores are set free from the sporangia, but when conditions are relatively dry, germ tubes are produced.

Antheridia and oogonia appear after sporangia have developed. They are buried in the host tissue, and tend to form in the flowers and axes of the inflorescences rather than in the leaves. The details of the sexual process[1] differ little from those of *Pythium de Baryanum*; periplasm is more abundant, and the functional female nucleus becomes associated with a deeply staining mass of cytoplasm in the centre of the ooplasm. Divisions take place in the oospore soon after the fusion of the male and female nuclei, so that there are some thirty-two nuclei in the resting oospore; there is evidence that the reducing division takes place when the fusion nucleus divides. Zoospores are set free on the germination of the oospore.

Allied species are stated to show variations in the sexual process. In *Albugo Bliti*[2] and *A. Portulacae*[2], the oogonia contain about 250 nuclei, the antheridia about thirty-five. Ooplasm is formed in the oogonium and the nuclei pass into the periplasm and divide there. Some fifty nuclei pass back into the ooplasm and, after a second nuclear division, many of the daughter nuclei degenerate. A number of nuclei enter from the antheridium, and the male and female nuclei then fuse in pairs.

PERONOSPORACEAE

The Peronosporaceae are obligate parasites in higher plants; sporangia develop in groups upon clearly differentiated sporangiophores, which emerge from the host in early stages of development and come to maturity in the air.

The mycelium appears as coarse hyphae in the intercellular spaces of the host; haustoria[3] penetrate the host cells. In most species they are short, vesicular or ovoid structures, but, in *Peronospora*, elongated and richly branched haustoria (fig. 50) are formed by some species; much damage is caused, and the host may be killed. The parasite may enter the perennating organs of the host, and pass the winter there; *Peronospora Ficariae*[4] enters the tubers of the celandine, and *Pseudoperonospora Humuli*[5] perennates in the stools of the hop.

[1] Wager, 1896; Davis, 1900; Krüger, 1910.   [2] Stevens, 1899, 1901, 1904.
[3] de Bary, 1863 i.   [4] Krüger, 1910.   [5] Ware, 1926.

Hyphae accumulate beneath the stomata, branch, and give rise to the rudiments of sporangiophores. The latter emerge in groups from the stomata, elongate, usually branch, and produce sterigmata at the ends of the branches. The tip of the sterigma swells, nuclei and cytoplasm pass into the enlargement, and, when this sporangium has reached its full size, communication with the sporangiophore is interrupted by the blocking of the lumen of the sterigma[1]. After the sporangium has fallen, it may liberate zoospores, or direct germination may take place; the zoospores resemble those of *Pythium*.

So far as it is known, the sexual process[2] agrees closely with that of *Pythium*. The wall of the oogonium may disappear soon after the oospore is ripe;

Fig. 50. *Peronospora calotheca* de Bary; richly branched haustoria, × 400; after de Bary.

in *Plasmopara* it persists after the tissue of the host has rotted; in *Sclerospora* the thick wall of the oogonium and that of the oospore grow together to form a common envelope.

Basidiophora entospora[3] (fig. 51 a) attacks *Erigeron canadense*; the elongated club-shaped sporangiophores bear a few sterigmata at the apex; each supports a broadly ovoid sporangium from which the zoospores escape, one by one.

Plasmopara viticola[4] is the cause of downy mildew of the grape. The sporangiophore consists of a main axis, bearing four to eight lateral branches; sporangia develop singly on short sterigmata. In water zoospores are soon liberated; they swim for about twenty minutes and then produce a germ tube; this abbreviated period of activity suggests that the tendency to produce zoospores is weakening. *Plasmopara densa*[5] does not form zoospores; the con-

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[1] Rostowzew, 1903.
[2] Wager, 1900; Stevens, 1902; Rosenberg, 1903; Ruhland, 1904.
[3] Roze and Cornu, 1869.
[4] Farlow, 1876.   [5] Ruhland, 1904.
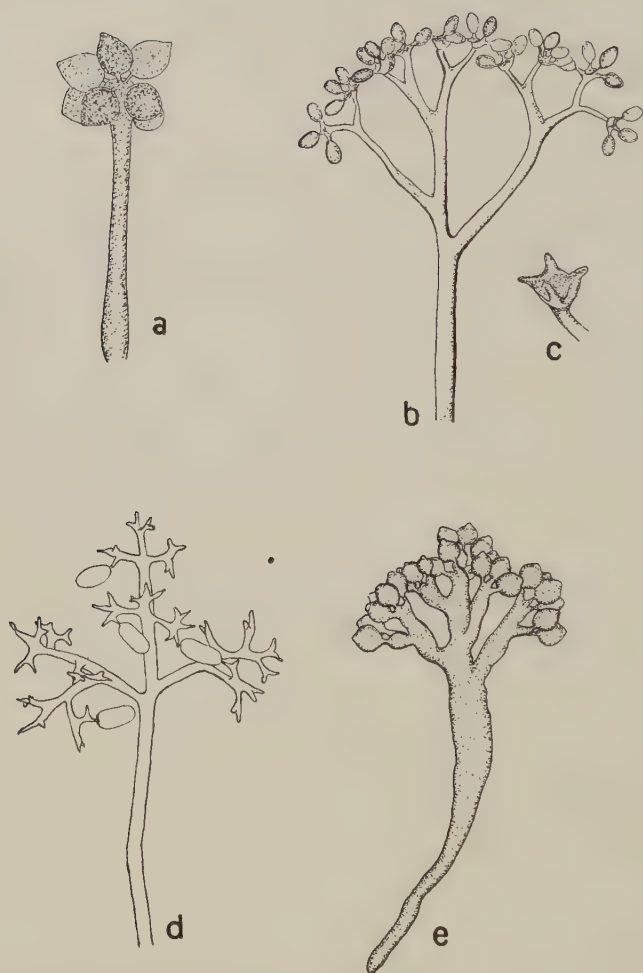
Fig. 51. *Basidiophora entospora* Roze & Cornu; *a*, sporangiophore, × 225; after Roze and Cornu. *Bremia lactucae* Regel; *b*, sporangiophore; after Milbraith; *c*, end of fertile branch, with sterigmata, × 190; after Schröter. *Peronospora leptosperma* de Bary; *d*, conidiophore, × 140; after de Bary. *Sclerospora graminicola* (Sacc.) Schröt.; *e*, sporangiophore, × 280; after Weston.

tents of the sporangium emerge as a whole, form a wall, and develop a germ tube.

Bremia lactucae[1] (fig. 51 *b*) occurs on lettuce. The sporangiophore has a long main axis with dichotomously or trichotomously arranged branches which may again branch. The fertile axes terminate in saucer-like expansions (fig. 51 *c*) with a few sterigmata around the margin; each bears a sporangium. In darkness, at low temperatures, and with sufficient moisture, zoospores may be produced; as a rule, however, direct germination occurs, the germ tube arising from the apex of the sporangium.

The tendency for the sporangium to become a conidium culminates in *Peronospora*, which is not known to form zoospores. The conidiophores (fig. 51 *d*) frequently show forked branching and a long main axis is not clearly distinguishable. Conidia, often violet in colour, develop in the same way as the sporangia of other members of the family. They fall off and germinate by the production of a germ tube from any point of their surface.

Pseudoperonospora Cubensis[2] attacks and kills cucumber plants. The sporangiophores branch like those of *Peronospora*, but the grey or smoky violet sporangia vary in their behaviour. They may give rise to zoospores, or they may function as conidia; when this occurs the germ tube may proceed from the apex of the sporangium, as in *Bremia*, or from some other point of the surface, as in *Peronospora*.

The sporangia of *Sclerospora graminicola*[3] (fig. 51 *e*) show similar behaviour. In this species, the sporangiophores develop and mature at night, apparently in relation to the better supply of moisture on the surface of the host at that time.

ZYGOMYCETES

The outstanding characteristic of the Zygomycetes is their method of sexual reproduction by the union of similar or slightly differentiated gametangia. Accessory multiplication is by non-motile spores developed in sporangia; usually the sporangium contains large numbers of spores, but small sporangia, known as

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[1] Schweizer, 1918; Milbraith, 1923.   [2] Rostowzew, 1903.
[3] Stevens, 1902; Kulkarni, 1913; Weston, 1923, 1924.

sporangiola, also occur, and contain one or a few spores each, or the sporangia are further modified to form conidia.

The Zygomycetes include between 200 and 300 species and may be divided as follows:

Accessory multiplication by sporangiospores MUCORALES
Accessory multiplication by conidia ENTOMOPHTHORALES

MUCORALES

The Mucorales[1] comprise about 150 species; they are saprophytic on many sorts of organic substrata, or, in a few cases, parasitic, chiefly on other members of the same alliance.

Multiplication is very largely by means of non-motile spores produced in stalked sporangia; they are carried by the air and form a germ tube on germination. The young sporangiophore arises as a branch of the mycelium, its apex becomes swollen to form the sporangium. The latter enlarges, receives nuclei, cytoplasm and food material, and is cut off by a wall. In the sporangia of the Mucoraceae and in the large sporangia of the Choanephoraceae this wall is dome-shaped from its initiation and is termed the **columella**. It remains as a conspicuous structure after the outer wall has broken away and the spores are shed.

Sexual reproduction is by the fusion of multinucleate gametangia which grow one towards another, or are formed in contact after the hyphae on which they develop have come into relation. The resultant **zygospore** produces a thick wall, which may be smooth or spiny, and is sometimes surrounded by a weft of vegetative hyphae. The branches on which the gametangia are borne are known as **suspensors**. Occasionally gametangia develop without fusion into **azygospores**.

The sexual method of reproduction was first observed by de Bary in 1864, in *Sporodinia grandis*, a form occurring on the pilei of Autobasidiomycetes, and zygospores were found to be readily obtainable in this species. In others, however, production of zygospores, though occasionally observed, proved exceedingly erratic; particular chemical substances or degrees of concentration were stated to be favourable to zygospore formation, but none of them proved reliable or stood the test of continued experiment.

[1] Lendner, 1908; Moreau, 1913 i; Namyslowski, 1920; Naoumoff, 1924; Nadson and Phillipov, 1925; Satina and Blakeslee, 1925.

The necessary condition was discovered by Blakeslee[1]. In the course of his investigations at Harvard he observed that, while zygospores of certain species, such as *Sporodinia grandis*, developed readily in pure culture from a single spore, yet in *Rhizopus nigricans* and many other species, zygospores were never obtained under such conditions, but only when a mass of spores from a culture which had borne gametangia was used for inoculation. Moreover, under these circumstances, zygospores were not obtained indiscriminately, but only along the line of junction of mycelia from different spores. In due course it was demonstrated that such species consist of two strains, or kinds of thalli, which, when grown apart, produce only sporangia, but which form zygospores when brought into contact. In some cases visible differences exist between the two strains, one being rather more luxuriant than the other; to the relatively well-developed strain the term (+) was applied, and the term (−) to the strain with which it produced zygospores. In other species, though a physiological difference evidently exists, since neither strain alone can produce zygospores, yet any morphological distinction is lacking, and a (+) or (−) strain can only be defined as one which produces zygospores in conjunction with the other.

Species in which conjugation depends on the interaction of two thalli are said to be **heterothallic**, while those which give rise to zygotes in mycelia from a single sporangiospore, and consist, therefore, of only one kind of thallus, are described as **homothallic**.

It is evident that the physiological distinction between (+) and (−) strains is equivalent to the difference of sex in other plants and animals, the homothallic mycelium being bisexual, like a fern prothallus, and the heterothallic, unisexual. It must be noted in this connection that, in heterothallic organisms, there is no difference between the sexual organs, and the distinction of sex is thus expressed in the simplest possible form, as the capacity to produce zygotes with a different, but not with a similar individual.

In some of the heterothallic species races have been found which respond neither to (+) nor to (−) mycelia, and may be described as **neutral**. In *Mucor Mucedo* the power of conjugation may be inhibited by cultivation under unfavourable conditions, and neutral strains are thus produced.

[1] Blakeslee, 1904.

The sexual response may be observed not only between (+) and (−) strains of the same species, but between (+) and (−) strains of different species, and even of different genera; under such circumstances gametangia are seldom cut off, and conjugation does not as a rule take place. The reaction has been used to discriminate (+) and (−) strains in forms in which no morphological distinction exists between the two. A similar response may occur between a homothallic species and the (+) and (−) strains of a heterothallic species.

On the germination of the zygospore a sporangium is usually formed, and the spores produced therein are the first stage of the new gametophyte.

The Mucorales may be divided as follows:

Sporangia globose or ovoid, usually containing numerous spores, sometimes one or a few; zygospore formed from the whole of the two gametangia	
Columella present, zygospore naked or invested by outgrowths from its own wall, or from those of the suspensors	
Principal sporangia containing numerous spores	
Sporangiola, if any, developed on lateral branches of principal sporangiophores	MUCORACEAE
Sporangiola developed independently	CHOANEPHORACEAE
Monosporous sporangiola (conidia) only	CHAETOCLADIACEAE
Columella absent; zygospore surrounded by a dense weft of vegetative hyphae	MORTIERELLACEAE
Sporangia elongated, springing from a swollen head, each containing a single row of spores; zygospore an outgrowth from one or both gametangia	CEPHALIDACEAE

MUCORACEAE

The sporangiophores arise as aerial branches from the mycelium; they are negatively hydrotropic, thus emerging from a liquid substratum, negatively geotropic, and, in some cases, positively phototropic to a marked degree. Branching of the sporangiophore may occur, as in *Sporodinia*, or the sporangiophores may be formed in bunches or corymbs, as in *Rhizopus*, or, as in *Mucor Mucedo*, they may grow up singly and unbranched; they are usually short, but in

Phycomyces nitens they may reach a height of thirty centimetres. The apex of the young sporangiophore enlarges to form the sporangium (fig. 52 *a*), and becomes crowded with cytoplasm, nuclei and food material. It is cut off by a dome-shaped wall, the columella (fig. 52 *b*), the position of which is at first delimited by a series of vacuoles; a plane wall is never present. Very soon, sometimes before the formation of the columella is complete, furrows from the periphery cut into the cytoplasm in a centripetal manner. They meet and fuse with furrows starting from the columella, and the spore plasm is thus cut into blocks of variable size. These undergo further segmentation; growth and sometimes nuclear division take place, and are fol-lowed by contraction; the spores round up and each develops a wall. The mature spore contains two nuclei in *Pilobolus crystallinus*, seven

Fig. 52. *Mucor hiemalis* Wehm.; *a*, young sporangiophore, before the sporangium is cut off; *b*, mature sporangium; *c*, sporangiophore and columella after the spores are shed; × 280; H. S. Williamson del.

or eight in *Mucor racemosus*, and a larger number in *Sporodinia grandis*. In *Sporodinia grandis* the process of spore formation is abbreviated, the protoplasm being cut into relatively large blocks which at once round up to form spores; they contain little reserve material and are short lived. In *Mucor Mucedo*, *Rhizopus nigricans* and others, segmentation is carried further, and smaller but still multinucleate spores are formed. In *Pilobolus crystallinus* cleavage is continued till the protoplasm is divided into uninucleate masses; these grow and become multinucleate; by further divisions they give rise to the binucleate spores[1].

In *Mucor* and other genera the quantity of fluid in the stalk and columella increases at maturity so that considerable pressure is set up; the thin wall bursts, setting free the spores and leaving a ring or collar around the distended columella (fig. 52 *c*). In *Pilobolus*, on the other hand, the upper part of the wall becomes firm in consistency and blue-black in colour, only a narrow zone about the base of

[1] Harper, 1899 ii; Schwarze, 1922.

the columella remaining delicate and colourless. Between the spores and the wall, and especially at the base of the latter, is a gelatinous layer which swells as water is absorbed from the substratum, so that the delicate lower region of the wall is broken, and the upper part of the wall, together with the mass of spores, is violently shot off. This will take place even in very dry air[1].
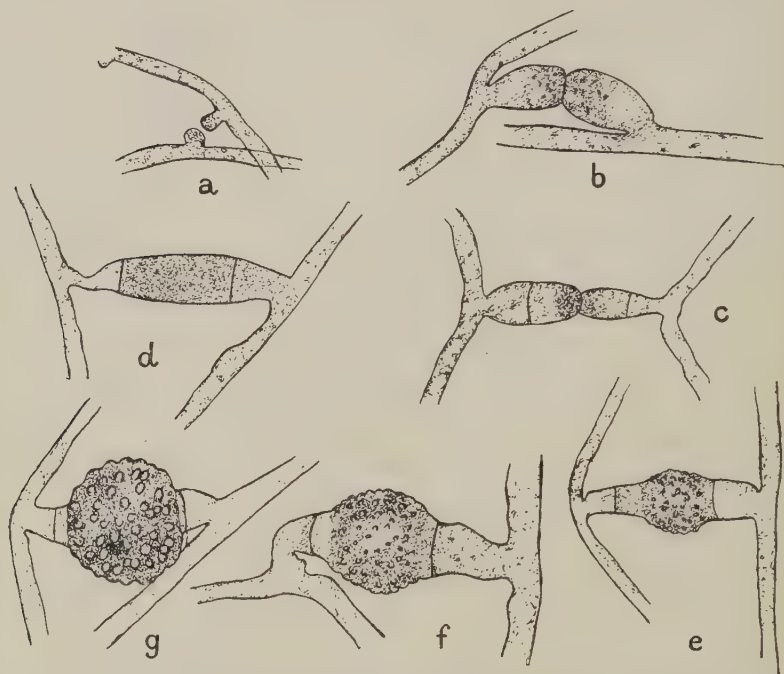
Fig. 53. *Mucor hiemalis* Wehm.; *a*, *b*, contact and growth of progametangia; *c*, progametangia divided to form gametangia and suspensors; *d*, conjugation; *e*, *f*, *g*, development of zygospore; × 280; H. S. Williamson del.

Large vesicles are developed on the sporangiophore, one just below the sporangium, and one at the further end; the upper apparently exercises an ocellar function[2].

In *Mucor Mucedo*[3] and *M. hiemalis*, when the mycelia of opposite strains come together, hyphae appear which are larger

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[1] We are indebted to Miss E. Green, M.Sc., for the observation that both *Mucor* and *Pilobolus* will discharge their spores in a desiccator.

[2] Buller, 1921.   [3] Blakeslee, 1904.

than the vegetative filaments, but more delicate than the stout sporangiophores, from which they also differ in not being phototropic. These hyphae approach one another, actuated apparently by a mutual attraction; they touch at or a little behind their tips, and, at the point of contact, each forms a club-shaped **progametangium** (fig. 53 *a*, *b*), which divides transversely to form the gametangium and the suspensor (fig. 53 *c*). The gametangia are more or less equal in size; in due course open communication between them is afforded by the dissolution of the intervening wall (fig. 53 *d*); the contents mingle, the nuclei fuse in pairs, the wall becomes greatly thickened and differentiated into layers, and the formation of the zygospore is complete (fig. 53 *e*, *f*, *g*). After a period of rest lasting from five to nine months the zygospore of *Mucor Mucedo* germinates, giving rise, under normal conditions, to a sporangium, the spores from which produce either only (+) or only (−) mycelia. If the development of the sporangium is
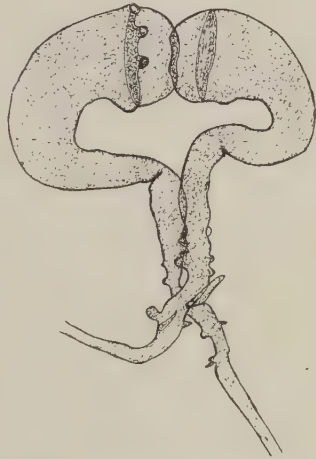
Fig. 54. *Phycomyces nitens* Kunze & Schmidt; interlocked branches bearing suspensors and gametangia, / 60; H. S. Williamson del.

interfered with, branches may be formed and more than one sporangium may result, but in every case the mycelia from sporangiospores originating from a single zygote are all (+) or all ( ), not mixed[1]. In such cases the fungus has been described as **heterosporangic** and **heterosporic**. In so far as heterothallism is equivalent to bisexuality, the condition corresponds to that in *Taxus*, where the sporophyte produces only micro- or only megasporangia.

Phycomyces nitens[2] is also heterothallic; when a hypha from a (+) mycelium meets one from a (−) mycelium, stout, lobed branches arise from each and become interlocked (fig. 54). Rapid growth brings about a separation of the subterminal regions, and

[1] Blakeslee, 1906 i.
[2] Blakeslee, 1906 i; Burgeff, 1914; Orban, 1919; Walter, 1921; Baird, 1924.

gametangia are cut off from the extremities of the interlocked hyphae, where the latter, as in other species, have been in contact throughout. The zygospores (fig. 55) are protected by dichotomously branched outgrowths arising from the suspensors; germination takes place after some months, and the germ tube gives rise to a sporangium in which both $(+)$ and $(-)$ spores are formed as well as spores which produce homothallic mycelia distinguished by contorted aerial branches and occasional homo-
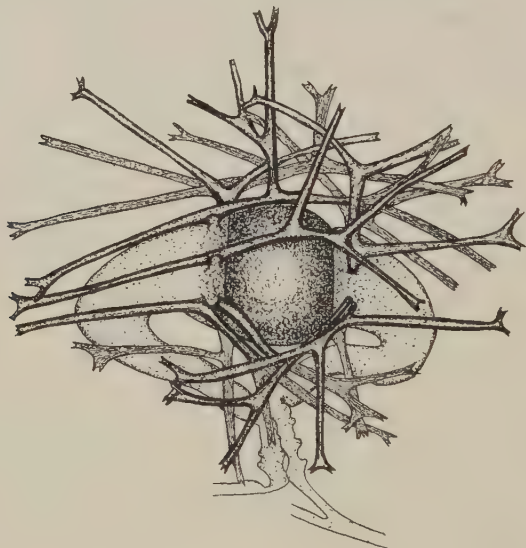
Fig. 55. *Phycomyces nitens* Kunze & Schmidt; mature zygospore, $\times$ 60; H. S. Williamson del.

thallic zygospores[1]. Both the sporangia of the homothallic mycelium and those derived from its zygospores give rise to $(+)$ and $(-)$ and homothallic spores.

None of the heterothallic forms among the mucors is known to be heterogamic. In *Rhizopus nigricans*[2], where there is no visible difference between the $(+)$ and $(-)$ mycelia, the gametangia often differ in size, but the larger gametangia occur indiscriminately on the $(+)$ and the $(-)$ mycelia, and the difference, which is clearly not one of sex, is presumably due to nutrition.

[1] Blakeslee, 1906 i.
[2] Blakeslee, 1907; McCormick, 1911.

Fig. 56. *Absidia glauca* Hagem; mature zygospore; after Lindner.
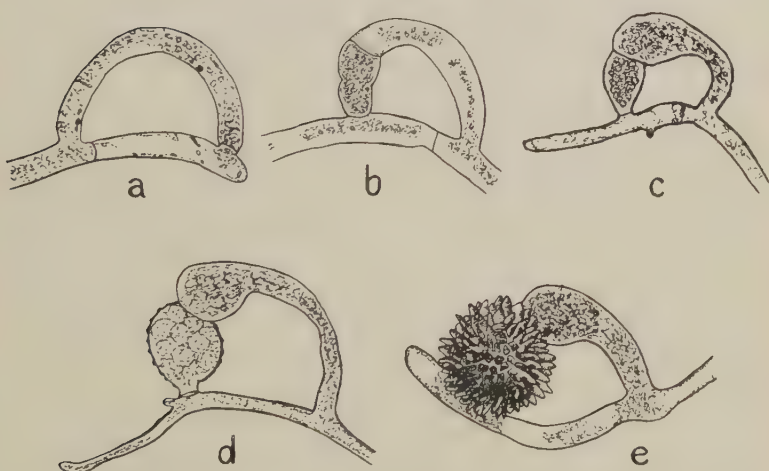
Fig. 57. *Zygorhynchus Moelleri* Vuill.; *a*, young progametangia; *b*, conjugation; *c, d, e*, development of zygospore; × 533; after Green.

Among homothallic moulds, *Sporodinia grandis*[1] and several others show no distinction between the gametangia, but in some species a regular difference in size exists; this is the case in *Absidia spinosa*, and here the characteristic appendages of the genus (fig. 56) are derived only from the suspensor of the larger gametangium.

In the genera *Zygorhynchus*[2] and *Dicranophora*[3] marked heterogamy is found. *Zygorhynchus Moelleri* occurs in soil; conjugation may take place between closely related branches. A septum is formed near the tip of an erect hypha; below the septum a branch grows out (fig. 57 *a*); it bends over and comes in contact with the side of the terminal segment where a second branch is formed. Both grow, the curved branch especially receiving abundant protoplasm; gametangia of unequal size are cut off, their contents mingle (fig. 57 *b*), the curved suspensor becomes greatly swollen (fig. 57 *c*, *d*), and empties its contents into the zygote. The zygote develops a spiny coat (fig. 57 *e*), and germinates after some months to give rise to a mycelium.

Fig. 58. *Dicranophora* sp.; *a*, formation of a progametangium from the larger and a gametangium from the smaller branch; *b*, young zygospore; after Blakeslee.

In *Dicranophora*, also, the gametangia are close together, and, while one remains scarcely wider than the hypha on which it is borne, the other becomes swollen, and a characteristic bulge develops on its stalk (fig. 58). The condition is essentially similar to that in *Zygorhynchus*, but the disproportion between the gametangia is greater.

It is a point of some interest that, when *Absidia spinosa* was hybridised with the heterothallic form known as *Mucor* V, the smaller of the gametangia of *Absidia* fused exclusively with those of the (+) strain, and the larger with those of the (−)[4]. Distinctions of sex are ordinarily concerned with the gametes, not with the organs which bear them; here no gametes are differen-

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[1] Dangeard, 1906; Keene, 1914; Robinson, 1926 i.

[2] Blakeslee, 1904, 1913; Dangeard, 1906; Moreau, 1911, 1912, 1913 ii; Kominami, 1914; Green, 1927.

[3] Blakeslee, 1904.   [4] Blakeslee, 1915, 1920; Burgeff, 1924.

tiated, but it is perhaps justifiable, in the absence of other evidence, to assume that the larger gametangium, like the larger gamete, is female. If so, the above observations connect the heterothallism of *Mucor* V and its allies with the ordinary, morphological differences of sex, and suggest that the (−) strain may properly be described as male, and the (+) strain as female.

CHOANEPHORACEAE

The members of the small family Choanephoraceae show a gradual transition from the sporangium to the conidium as a unit of accessory multiplication. The sporangia are produced both singly, and in groups on rounded heads; to the latter form the generic name *Oedocephalum* was given before its true position was understood. In *Blakeslea*[1] the single sporangia are spherical; some possess a well-marked columella and many spores, while in others the spores are few and the columella small or obsolete (fig. 59). On the rounded heads from twelve to forty sporangiola are borne; the heads are often arranged in groups of ten or more, so that conspicuous fructifications are produced. Each of the sporangiola on these heads usually contains three spores, rarely four or six. The size of the spore varies inversely with the size of the sporangium, so that the largest spores are those developed in the smallest sporangiola on the oedocephaloid heads, and a complete transition series is available from the largest to the smallest size.

In *Cunninghamella*[2] and *Choanephora*[3] similar oedocephaloid heads are produced, but the sporangiolum containing three or four spores is replaced by a single cell. Careful manipulation in *Choanephora* reveals that this cell is surrounded by a partly separable membrane, so that it may be regarded as the single sporangiospore of a sporangium which falls off as a whole, and has, in effect, become a conidium.

When *Cunninghamella echinulata* was first observed in the oedocephalid form, it was placed in the *Fungi imperfecti*; it was transferred[4] to the Mucorales on the ground of its non-septate mycelium and of its liability to be attacked by *Piptocephalis*, a

[1] Thaxter, 1914 ii.
[2] Matruchot, 1903; Blakeslee, 1904, 1906 ii; Thaxter, 1914 ii; Burger, 1919; Blakeslee, Cartledge and Welch, 1921; Torrey, 1921.
[3] Dastur, 1920.   [4] Matruchot, 1903.

member of the Cephalidaceae and an obligate parasite on the Mucorales. Zygospores were not known till 1904 when their dis-
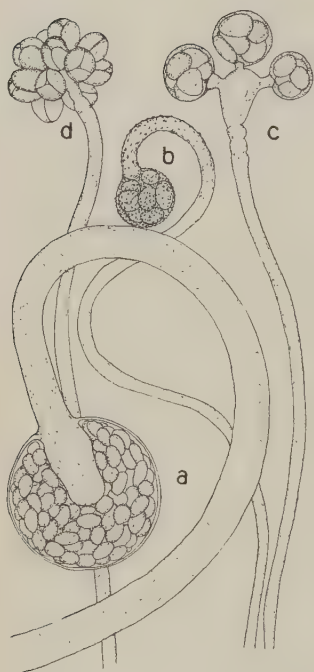
Fig. 59. *Blakeslea trispora* Thaxter; *a*, well developed sporangium with numerous spores; *b*, smaller sporangium; *c*, group of sporangiola with a few spores each; *d*, characteristic oedocephaloid head with three-spored sporangiola; after Thaxter.
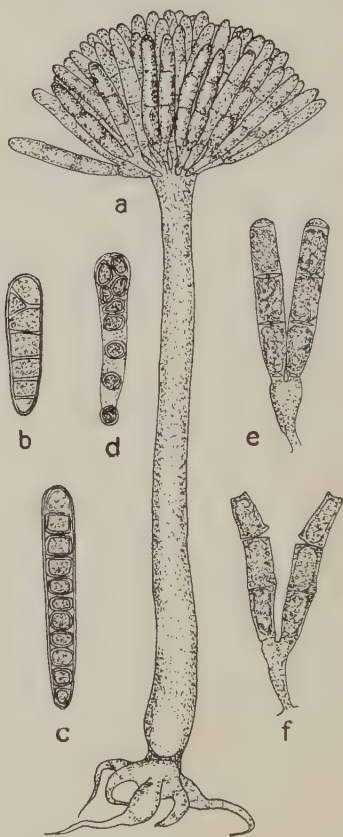
Fig. 60. *a*, *Syncephalis pycnosperma* Thaxter; nearly mature sporangiophore with numerous sporangia. *b*, *c*, *d*, *Syncephalastrum racemosum* Cohn; stages in the separation of spores. *e*, *f*, *Syncephalis pycnosperma* Thaxter; stages in the separation of the spores. After Thaxter.

covery[1] confirmed the previous ingenious diagnosis. The mycelium is in some cases heterothallic, and the zygospores are without appendages.

[1] Blakeslee, 1904.

CHAETOCLADIACEAE

The family Chaetocladiaceae includes a single genus, *Chaeto-cladium*[1], which may develop saprophytically, or may parasitise other Mucorales. Conidia are produced singly on richly branched hyphae, and zygospores with sculptured walls have been observed.

MORTIERELLACEAE

Mortierella and its allies[2] occur chiefly on decaying organic substances, but *M. echinulata* is parasitic on the larger moulds. The mycelium is slender, dichotomously branched and frequently anastomosing. The sporangia arise singly on racemose or cymose branches; the spores are usually numerous in each sporangium and round or oval in form. In *M. fusispora*, however, the spores are spindle shaped; in *M. polycephala* and other species they may be reduced to four in each sporangium, and to one or two in *Haplosporangium bisporale*, while, in *H. decipiens*, the sporangia are always monosporous, a conidial condition having been attained. The basal wall of the sporangium is flat, so that no columella is produced.

The zygospore is formed as in the Mucoraceae, but its wall consists of a single layer, and it is surrounded and protected by branches from the suspensors or from the hyphae on which they are borne.

CEPHALIDACEAE

Among the Cephalidaceae all known species of *Piptocephalis*, *Syncephalis*[3] (fig. 60 *a*) and *Dispira*[4] are obligate parasites on the Mucorales; the remaining members of the family are saprophytes on dung or other substances. They are characterised, in respect of their accessory methods of reproduction, by the numerous, narrow sporangia, in each of which the spores occur in a single row.

In *Syncephalastrum*[3], a saprophytic genus of tropical origin, the fertile branch ends in a spherical head from which sporangia radiate in all directions, forming an *Aspergillus*-like fructification. Each sporangium is budded out from the head as a continuous,

[1] Burgeff, 1920.   [2] Thaxter, 1914 ii.
[3] Thaxter, 1897.   [4] Thaxter, 1895 iii.

cylindrical cell; its contents divide, and around each separate mass
a wall is formed (fig. 60 b, c, d); these spores are set free by the
disappearance of the sporangial wall, which shrivels and breaks up.
By careful manipulation of immature material, however, the spores
can be squeezed out and the sporangial wall left intact, showing
that the units of multiplication are sporangiospores, not exogen-
ously formed conidia.

In *Piptocephalis* and *Syncephalis*, as in *Syncephalastrum*, the
protoplasm of the sporangium is at first continuous; in *Syncephalis*
the spores are formed by transverse
septation, and each closely adheres
to the adjacent segment of sporangial
wall, so that the subsequent de-
liquescence of the intermediate zones
transforms the sporangium into a row
of thick-walled spores (fig. 60 e, f).

As in most of the Mucorales,
the gametangia in *Piptocephalis* are
similar in form and size; the zygote,
however, arises as an outgrowth
from the point of fusion; it develops
a thick and spiny wall.

Fig. 61. *Syncephalis nodosa* Van
Tieghem; a, gametangia seen from
above; b, the same a little later,
with a zygospore growing out from
the coiled gametangium; c, d,
later stages, viewed laterally; after
Thaxter.

In *Syncephalis nodosa* (fig. 61)
sexual reproduction is initiated by
the association of a pair of hyphae, one of which is twisted about
the other; the end of the relatively straight hypha becomes swollen
to form a gametangium and is cut off by a wall; the tip of the
enveloping hypha winds around this swollen extremity, and a
septum separates the last turn of the spiral from the rest, so that
a second gametangium is produced. The wall between the two
gametangia now breaks down and conjugation takes place; the
contents of the swollen head pass into the spiral and a zygospore
is budded out from the latter in the neighbourhood of the septum.
The stalk below the septum gives rise to bladder-like outgrowths.
In this case, and apparently in other species of *Syncephalis*, there
is well-marked differentiation of the gametangia, the spiral branch,
since it gives rise to the zygote, being presumably female.

ENTOMOPHTHORALES

The Entomophthorales include some fifty species which have many characters in common and are classified in a single family, the Entomophthoraceae. Most of the species are parasites on insects, a few occurring saprophytically on dung and other substrata, possibly, in some cases, on insect remains contained therein. The mycelium is not infrequently septate, with fatty contents; it produces large conidiophores from the ends of which conidia are violently discharged. The conidia are large, colourless and often multinucleate; they may be regarded here, as elsewhere, as modified sporangia.

In sexual reproduction fusion takes place between segments of the mycelium; the zygospore is formed by the enlargement of one or both, or as a lateral outgrowth into which their contents pass. It germinates after a period of rest and gives rise to a mycelium bearing conidia. The formation of similar resting cells without fusion is not uncommon, such structures being known as azygospores.

Entomophthoraceae

The species of *Entomophthora*[1] and *Empusa*[2] are responsible for serious epidemics among insects, in many cases among those injurious to plants or animals; the germ tube from the conidium penetrates the skin of the host and gives rise inside its body to numerous, irregular segments which multiply by budding, or to a branched, anastomosing, often septate mycelium. At about the time of the death of the host the mycelium, if present, breaks into short, thin-walled, multinucleate portions known as **hyphal bodies**. These, if conditions are not suitable for immediate growth, pass into a resting stage during which the wall becomes thickened, so that they may be described as chlamydospores; under the influence of warmth and moisture renewed development takes place with great rapidity. The germinating chlamydospore, or the unaltered hyphal body, sends to the surface of the host a long conidiophore, which, in *Entomophthora*, sometimes undergoes septation, forming a series of usually binucleate cells. The conidium de-

[1] Thaxter, 1888; Riddle, 1906; Molliard, 1918.
[2] Thaxter, 1888; Riddle, 1906; Majmone, 1914.

veloped at the end of this branch contains a single nucleus, and is shot off to a distance of two or three centimetres. When conditions of growth are favourable, the single, primary hypha may
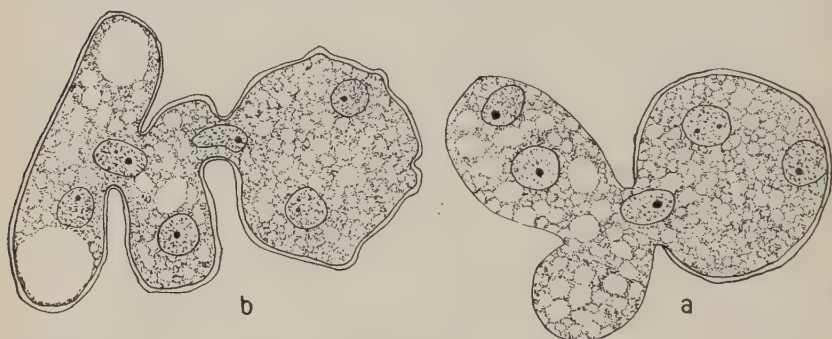
Fig. 62. *Entomophthora Americana* Thaxter; *a*, fused hyphal bodies with round zygospore growing from point of contact; *b*, same, round zygospore arising from the side of one of the hyphal bodies; × 650; after Riddle.
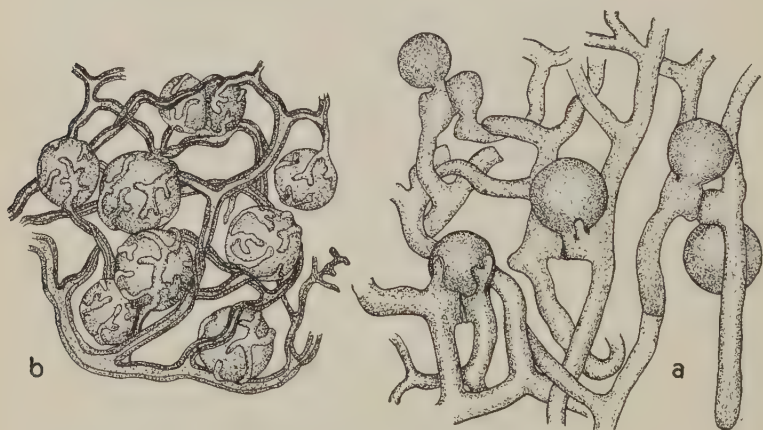
Fig. 63. *Entomophthora rhizospora* Thaxter; *a*, young zygospores; *b*, resting zygospores; × 170; after Thaxter.

branch again and again, each ultimate branch becoming a conidiophore.

The hyphal bodies are also concerned in sexual reproduction. In *Entomophthora Americana* two may fuse near their tips (fig. 62 *a*) and the young zygote buds out from the point of fusion as

in *Piptocephalis*; alternatively, if the hyphal bodies fuse side by side, an H-shaped figure is produced (fig. 62 *b*), and the nuclei and most of the cytoplasm of both bodies pass into an outgrowth from one of them at a point remote from the point of fusion. In either case the young zygospore is cut off by a wall, and passes into a resting condition (fig. 63 *b*) which lasts till the succeeding summer. Nuclear fusion has not been observed, but may occur on germination.

The conidiophores of *Empusa* differ from those of *Entomophthora* in being always unbranched (fig. 64); the nuclei are smaller
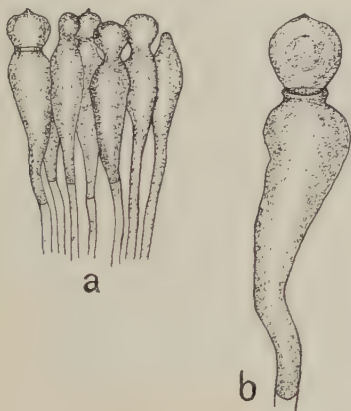
Fig. 64. *Empusa Muscae* Cohn; *a*, group of conidiophores, × 185; *b*, single conidiophore; × 350; after Thaxter.
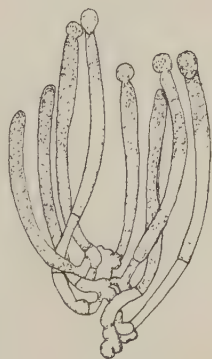
Fig. 65. *Conidiobolus utriculosus* Brefeld; group of conidiophores, × 80; after Brefeld.

and more numerous, each conidium containing twelve to fifteen fusion between hyphal bodies has not been observed, but single hyphal bodies bud out azygospores into which the contents pass; a thick coat is formed and a resting stage entered, as in the zygospores of *Entomophthora*.

Conidiobolus utriculosus[1] is a parasite on the sporophores of *Auricularia* and its allies, and *C. villosus*[2] on *Hypochnus*. The conidia (fig. 65) grow readily upon nutrient media, forming branched and rarely septate hyphae; these give rise to conidia which, instead of germinating at once, may be transformed by the

[1] Brefeld, 1884.   [2] Martin, G., 1925.

thickening of their walls, into resting cells, or into hyphal bodies. Conjugation of the latter and the formation of zygospores has been recorded for *C. utriculosus*.

Completoria complens[1], the only species of this genus, forms brown spots on the prothalli of ferns. It exists inside the cells in the form of short, thick hyphae, or hyphal bodies, which may give rise either to conidia or to resting spores. The sexual origin of the latter has not been demonstrated.

The subterranean genus *Endogone*[2] had been variously placed in the Gasteromycetales, in the Tuberales, between the Phycomycetes and Ustilaginales, and in the Hemiasci, a group which included
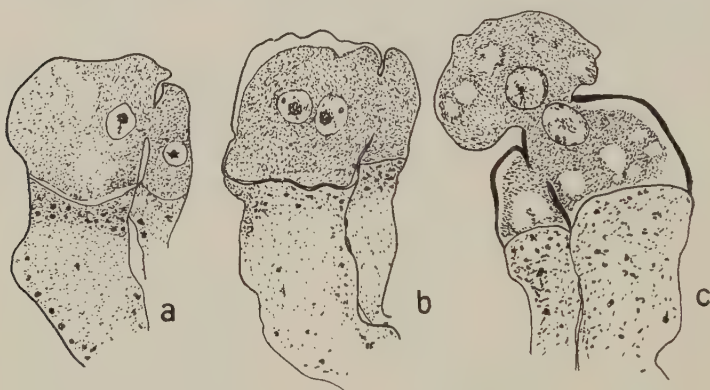
Fig. 66. *Endogone lactiflua* Berk.; *a*, *b*, conjugation; *c*, development of zygospore; after Bucholtz.

Dipodascus and *Protomyces*, before fuller investigation enabled it to be referred to its present position. In *Endogone lactiflua* the young fruit body consists of a mass of interwoven hyphae, the outermost of which combine to form a peridium or protective layer. From the inner filaments gametangia develop as multinucleate out-growths of unequal size. In each a single, large nucleus appears and a terminal, uninucleate portion is cut off by a wall. The gametangia fuse (fig. 66 *a*, *b*), the zygote grows out from the larger of the two, and into it both nuclei pass (fig. 66 *c*); their fusion has not been seen. Each zygote is surrounded and protected by a sheath of vegetative hyphae.

[1] Leitgeb, 1882.   [2] Bucholtz, 1912; Fischer, 1923 ii.

The best-known species of *Basidiobolus*[1], *B. ranarum*, occurs on the excrement of frogs; it possesses a richly branched mycelium of large, colourless hyphae which become increasingly septate as development proceeds, and break up into hyphal bodies only under abnormal conditions. Large, spherical conidia are discharged from slender conidiophores (fig. 67), the region just below the conidium becoming swollen and cut off by a wall. In sexual reproduction
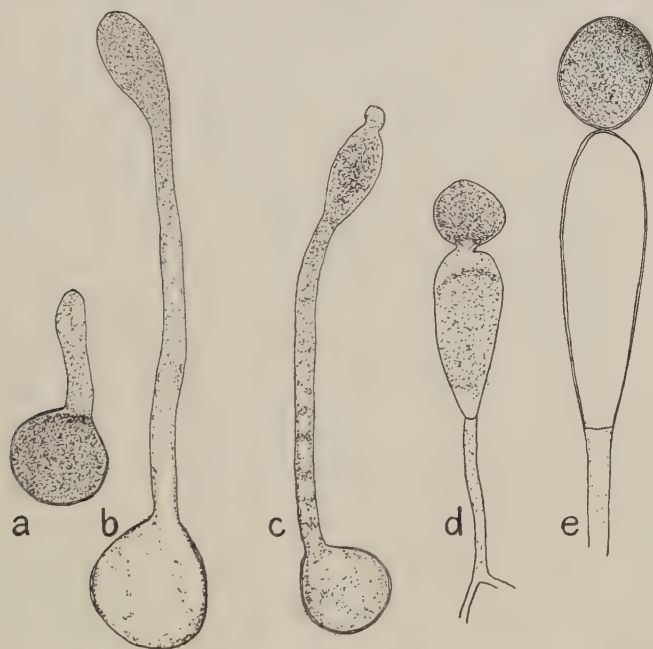
Fig. 67. *Basidiobolus ranarum* Eidam; *a*, germinating conidium; *b*, *c*, same preparing to give rise to a new conidium at the end of the germ tube; *d*, *e*, later stages in the development of the conidium; × 210; H. S. Williamson del.

two adjacent, uninucleate cells, the gametangia, send out short branches into which the nuclei pass. Meantime the wall between the cells (fig. 68 *a*) has broken down, and one of them has enlarged considerably. The nuclei divide, one daughter nucleus in each case remains in the branch, the other passes back into the gametangium; the branches are cut off and play no further part in development. The nucleus of the smaller gametangium

[1] Fairchild, 1897; Fries, 1899; Olive, 1907.

now moves into the larger; the nuclei lie side by side (fig. 68 *b*) for a time and then fuse; the zygospore surrounds itself by a wall and, on germination, gives rise to conidia.

It will be seen that *Basidiobolus* and *Endogone* differ from the
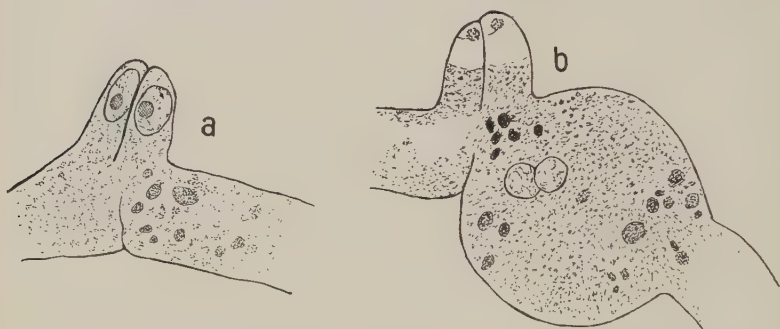
Fig. 68. *Basidiobolus ranarum* Eidam; *a*, fused gametangia; *b*, association of nuclei in swollen megagametangium; × 1110; after Fairchild.

other genera in that the mycelium does not normally break up into hyphal bodies. In *Basidiobolus*, and to a less extent in *Endogone*, the gametangia are differentiated from the vegetative cells; possibly forms like *Entomophthora*, where fusion is between hyphal bodies, should be regarded as pseudapogamous.

ASCOMYCETES

The Ascomycetes include over 15,000 species, all of which, excepting only the yeasts, possess a well-developed mycelium of branched and septate hyphae. The cells of the mycelium may be uninucleate, as in the Erysiphaceae and in species of *Chaetomium* and *Sordaria*, or they may contain a few or several nuclei; where growth is energetic, the rapid succession of nuclear divisions often causes the nuclei of coenocytic elements to be arranged in pairs[1].
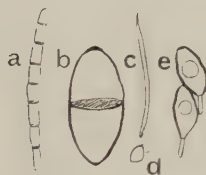
Fig. 69. Spores of *a, Geoglossum difforme* Fr.; *b, Delitschia furfuracea* Niessl.; *c, Rhytisma Acerinum* (Pers.) Fr.; *d, Chaetomium Kunzeanum* Zopf; *e, Podospora minuta* (Fuck.) Wint.; × 250.

Fig. 70. *Pleospora* sp.; germinating spores, × 500.

Multiplication may take place by means of conidia[2] and chlamydospores, but the characteristic method of reproduction is by ascospores, that is, by spores produced in the interior of a specialised mother cell, or ascus.

The Ascospores. The ascospores are usually elliptical in outline, but in some species spherical, and in some long and narrow (fig. 69); they contain densely granular cytoplasm and in many cases oil drops. The epispore may be smooth or sculptured; hyaline or opaque, colourless or variously coloured. The young spore is always unicellular and uninucleate; but before the spore is set free, the nucleus may divide and wall formation may follow, the mature spore consisting of a row or mass of cells (fig. 70). Each cell of a multicellular spore is usually capable of putting out a separate germ tube.

[1] Welsford, 1916.　　　[2] Klebahn, 1918.

The Ascus. The ascus, or spore mother cell, is a globose, ovoid, club-shaped, or almost cylindrical organ with a narrow, somewhat elongated base. Before reaching maturity it contains a single nucleus which undergoes three karyokinetic divisions, giving rise to eight daughter nuclei (fig. 71), around which the spores are

Fig. 71. *Humaria rutilans* (Fr.) Sacc.; hymenial layer showing asci and paraphyses in various stages of development, × 400.

delimited by a process of free cell formation. All the cytoplasm of the ascus is not included in the spores; the remainder constitutes the **epiplasm**, and becomes rich in food substances and glycogen. The glycogen in slender asci, such as those of *Peziza vesiculosa*, is usually confined to the region below the spores, while in broader asci it surrounds the spores also[1]; it exerts little or no osmotic pressure, but is capable of being rapidly transformed into sugars

[1] Walker and Andersen, 1925.

of high osmotic value. Such a transformation and the consequent absorption of water may be responsible for the bursting of the ascus and the violent ejection of the spores. There is evidence that the amount of glycogen present may be a factor in determining the distance to which the spores are thrown. Glycogen, or similar substances, the alteration of which results in a change of osmotic pressure, may play an important part in many of the rapid cell expansions characteristic of fungi.

In most of the Ascomycetes the mature ascus contains eight spores, but, in some, though eight nuclei are produced, spores are formed round only one or a few; and in some the three original nuclear divisions are succeeded by others, spores being formed around sixteen, thirty-two, or a larger number of nuclei. Thus a single spore is sometimes developed in *Tuber*, two is the regular number in *Phyllactinia*, and four in many of the Laboulbeniales, in *Bulgaria polymorpha* and in *Sordaria maxima*; there are sixteen or thirty-two in species of *Rhyparobius*, sixteen to sixty-four in *Philocopra pleiospora*, and in *Philocopra curvicolla* one hundred and twenty-eight. In the simplest genera spores are liberated by the disintegration of the ascus wall, and, if a definite sheath surrounds the asci, remain for a time enclosed by its outer layers; in the Discomycetes and Pyrenomycetes, however, the ascus opens explosively, by an irregular tear, or by dehiscence along a definite line (figs. 72, 73), and the spores are shot out in a jet of liquid, while the deflated ascus sinks back to about half its size. Where the asci are enclosed in a fructification with a long neck, they may deliquesce to form a mucilaginous mass which readily absorbs water and expands, being squeezed up the neck and exuded at the ostiole. In other flask-shaped fructifications the ascus elongates to reach the ostiole and the spores either float near the tip of the ascus in its fluid contents or are attached to the apex and to one another by cell prolongations or strands of wall material. Elongation of the ascus before the discharge of the spores is also found in the cup-shaped fructifications of the Ascobolaceae.

In forms with an exposed hymenium the asci, under damp conditions, discharge their spores in succession; but, on a quiet, dry day, any disturbance causes large numbers of ripe asci to eject their contents together, so that a cloud of spores is visible to the naked eye. This phenomenon, which is known as puffing, may be

Fig. 72. *Mitrula laricina* Mass.;
development and ejection of
biseriate spores, × 600.

Fig. 73. *Sepultaria coronaria* Mass.;
uniseriate spores; ascus opening by
a lid; branched, septate, clavate para-
physes; × 600.

brought about by shaking the fructifications, or even by the currents of air set up by walking past them. It can be induced, when ripe asci are lying in water, by exposing them suddenly to the action of glycerine or alcohol, and is due to alterations of pressure affecting all asci at the same stage of development.

Fig. 74. *Sordaria* sp.; ascocarp in longitudinal section showing asci, paraphyses and periphyses, × 400.

The Ascocarp. In the Endomycetaceae and Saccharomyceta-ceae the asci develop singly; in the great majority of families they arise in associated groups, and are protected by a common wall of sterile filaments known as the **peridium**; in this way a definite fructification, the **ascocarp** or **ascophore**, is formed. The young ascocarp is globose and usually completely closed; it may retain this form at maturity, opening only by the decay or irregular

splitting of its walls; it may assume a flask-shaped outline, opening by a terminal pore, the **ostiole** (fig. 74); or it may spread out to form a cup in the concavity of which the asci are fully exposed. The cup-shaped ascocarp is known as an **apothecium**, to the other forms the term **perithecium** is applied. In some of the simpler perithecia the asci are irregularly disposed, in the rest, and in all apothecia, they are arranged in parallel series (fig. 71) and are intermingled with paraphyses.
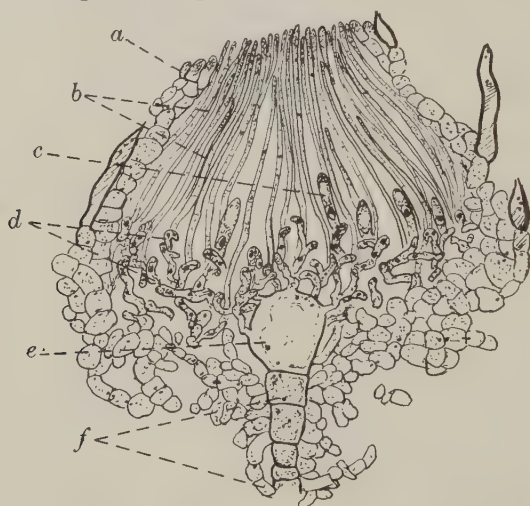
Fig. 75. *Lachnea stercorea* (Pers.) Gill.; ascocarp in longitudinal section showing young asci and paraphyses; the oogonium is still recognisable; × 160. *a*, sheath; *b*, paraphyses; *c*, ascus; *d*, ascogenous hyphae; *e*, oogonium; *f*, stalk of archicarp.

The paraphyses are slender filaments of about the same length as the asci; they develop earlier than the latter (fig. 75), usually forming a wedge-shaped group, and their growth forces open the apothecium. They are cylindrical, pointed or club-shaped, and often contain bright coloured granules. The peridium varies greatly in thickness; hairs and other appendages are in some cases developed from its outer cells. Filaments known as **secondary mycelium**[1] grow down into the substratum and supply food.

Sexual Reproduction. The Ascomycetes show a well-marked alternation of generations modified by the wide occurrence of

[1] This meaning of the term must not be confused with the significance more recently given to it in Basidiomycetes, cf. p. 247.

apogamy in the group. In forms where normal fertilisation is still retained the mycelium produced on the germination of the spores gives rise to the sexual organs. These show considerable variety of form, and are, in most cases, clearly differentiated into male and female structures. The male branch consists of an antheridial hypha or stalk, and a terminal antheridium which, in some of the more complex forms, is detached and carried by the wind or otherwise as a spermatium. The female branch, or **archicarp** (fig. 75), possesses a stalk of one or more cells, bearing the oogonium. In many species the latter gives rise to a trichogyne by means of which communication is established between the oogonium and antheridium. Often the oogonium becomes septate after the fertilisation stage, and sometimes several of its cells become continuous at an earlier period and constitute together an **oogonial region**. From the oogonium, or oogonial region, a number of filaments, the **ascogenous hyphae**, bud out. These receive the oogonial contents, and, at their tips, give rise to asci, in the first two nuclear divisions in which meiosis takes place. The ascogenous hyphae thus form the sporophyte, while the vegetative filaments, on which the sexual organs are borne, are gametophytic. The peridium and paraphyses, derived from the vegetative filaments, are part of the gametophyte, which also gives rise to the conidia and chlamydospores. These accessory spores play no part in the alternation of generations, but serve for the rapid spread of the gametophyte; it is the ascospores alone which correspond to the asexual spores of higher plants.

In the large majority of species possessing male and female organs, these are produced on the same mycelium, but, in *Ascobolus magnificus*[1], in certain of the Laboulbeniales[2], and also in the genus *Glomerella*[3], there are individuals of two strains, so that the fungus may be regarded as heterothallic, or, when one strain bears male and the other female organs, as dioecious. In *Glomerella* perithecia are produced both on (+) and on (−) strains, but are more abundant where these meet, indicating that some stimulus, whether sexual or otherwise, is provided by their union. Moreover asci in perithecia on a (+) or a (−) mycelium produce only corresponding spores, while those formed in perithecia along the line of junction may contain spores of both kinds. In *Diaporthe per-*

[1] Dodge, 1920.   [2] Thaxter, 1896 i, 1908.   [3] Egerton, 1914.

niciosa[1] a somewhat different phenomenon has been reported. It is not uncommon for mycelia growing and meeting in the same dish to refuse to grow through one another; this aversion is doubtless associated with the staling of the medium by the hyphae which have already covered it. But in *Diaporthe* there are not only strains which show aversion, but others, not morphologically different from these, which readily intermingle, and new strains of either type may arise from the other. The distinction between such strains is not apparently sexual or associated with sex, and they are heterothallic only in the literal sense.
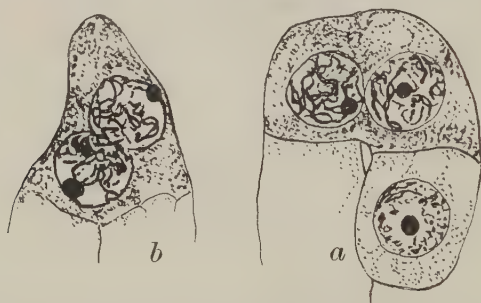
Fig. 76. *Humaria rutilans* (Fr.) Sacc.; *a*, ascogenous cell containing two nuclei cut off from the uninucleate terminal cell and stalk; *b*, fusion in the ascus, the nuclei are just passing into synapsis; both × 1875.

Cytology. Thanks to the researches of de Bary and others, sexual organs had been reported in a number of Ascomycetes during the latter half of the nineteenth century, and before the study of nuclear detail was undertaken. Nuclear fusion, however, was first observed by Dangeard in 1894, not in the oogonium, but in the ascus. He found[2] that, in *Peziza vesiculosa* and other species with a well-developed fructification, the tip of the ascogenous hypha bends over, two nuclei pass into the bent region and there divide simultaneously (fig. 80), the curved, subterminal segment retaining one daughter nucleus of each division (fig. 76 *a*), while the others are cut off by transverse walls, one in the terminal cell or tip, the other in the basal region or stalk, below the curve. The two nuclei in the subterminal cell fuse (fig. 76 *b*), and this cell becomes the ascus. Dangeard's observations have been widely

[1] Cayley, 1923 ii.　　　[2] Dangeard, 1894 ii.

confirmed, and it would appear that, apart from occasional trinu-
cleate and quadrinucleate cases, all asci borne on ascogenous
hyphae are binucleate at their first formation; in many species,
however, the bending over of the ascogenous hypha does not take
place; two nuclei simply pass into the end cell of the filament,
which is then cut off by a wall and
forms the ascus. Among Ascomy-
cetes anastomoses are common, not
only between vegetative filaments,
but between the tip and stalk cells
of ascogenous hyphae when the
bending over of the ascus occurs.
Often the nucleus of the stalk passes
into the tip, which having thus ac-
quired two nuclei, grows on to form
a second ascus[1]; a third (fig. 77) and
a fourth may arise in the same way.
The method of ascus formation has
by some authors[2] been compared
with the production of clamp con-
nections in the secondary mycelium
of the Basidiomycetes, but a study
of development shows that, whereas
the ascus is formed by the bending
over of a hypha of which the beak
is the terminal cell, the clamp con-
nection is a lateral outgrowth. Clamp

Fig. 77. *Humaria rutilans* (Fr.)
Sacc.; an ascus (*a*) the terminal cell
connected with which has con-
tinued its growth and given rise to
another ascus (*b*) from the terminal
cell of which a third ascus (*c*) has
arisen, × 1250.

connections have been reported in the ascogenous hyphae of lichens[3]
but only near the region of ascus formation, where the proliferation
of stalk and terminal cell may produce a similar appearance.

The year after Dangeard's discovery of the binucleate ascus,
his observations and those of de Bary were confirmed by Harper
for the hop mildew, *Sphaerotheca Humuli* (fig. 78). Harper[4] saw
the development of a uninucleate antheridium and a uninucleate
oogonium; he observed the passage of the male nucleus into the
oogonium and its fusion with the female nucleus; after fertilisation

[1] Fraser, 1908; McCubbin, 1910; Brown, W. H., 1910, 1911; Claussen, 1912.
[2] Claussen, 1912; Kniep, 1916; Bensaude, 1918; cf. p. 247.
[3] Moreau and Moreau, 1922; Moreau, 1925.   [4] Harper, 1895.

the oogonium underwent septation, giving rise to a row of cells, the penultimate of which contained two nuclei and, when these had fused, developed into the ascus. In the life history of this fungus there occurs, then, not only the fusion of sexual nuclei usual in other plants and animals, but a second fusion, that in the young ascus, so that the ascus nucleus is regularly tetraploid. These observations have been confirmed in several other Asco-mycetes, and it has moreover been shown that, while the first two
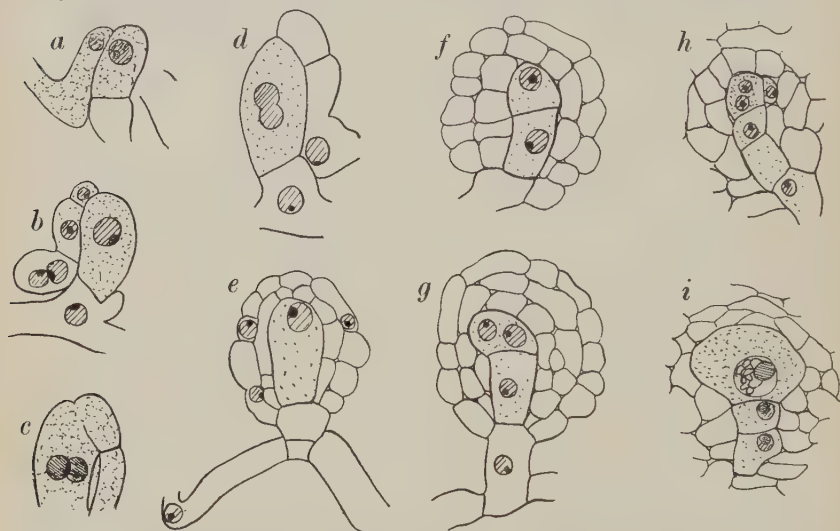
Fig. 78. *Sphaerotheca Humuli* (DC.) Burr.; *a* and *b*, antheridial and oogonial hyphae; *c*, entrance of male nucleus; *d*, fusion in oogonium, antheridium without nucleus; *e*, fusion nucleus in oogonium; *f* and *g*, septation of oogonium; *h*, two nuclei in ascus; *i*, ascus after nuclear fusion; after Harper.

divisions in the ascus constitute a meiotic phase (fig. 80 *b*, *c*), a second reduction[1], known as **brachymeiosis**, takes place in the third division (fig. 79). Thus the nuclei of the ascogenous hyphae after fertilisation are diploid, the ascus nucleus before division is tetraploid, after the first two mitoses the ascus contains four diploid nuclei, and, after the third mitosis, there are eight haploid nuclei in the ascus about which the spores are formed. The allelo-morphs which are to be separated in brachymeiosis may become associated during the second division (fig. 79 *b*).

[1] Maire, 1905; Dangeard, 1907; Fraser, 1908; Fraser and Welsford, 1908; Fraser and Brooks, 1909; Tandy, 1927.

Fig. 79. *Ascobolus furfuraceus* Pers.; *a*, early anaphase of the first division in ascus showing 14 of the 16 daughter chromosomes; *b*, metaphase of the second division showing four chromosomes; *c*, third division showing four; after Dangeard.

Fig. 80. *Humaria rutilans* (Fr.) Sacc.; *a*, ascogenous hypha showing sixteen chromosomes in each nucleus, × 1950; *b*, fusion nucleus of ascus with double spireme, × 1300; *c*, fusion nucleus of ascus showing sixteen gemini, × 1950.

The constancy of the binucleate condition in the young ascus is remarkable and is perhaps concerned with the establishment of a satisfactory quantitative relation between the nuclear substance and the cytoplasm[1]; fusion is probably due to the close association of the nuclei at a time when they are preparing for meiosis and their nuclear membranes are breaking down; in some cases synapsis has actually begun before nuclear fusion is complete (fig. 76 b).

When the study of forms grown in artificial culture became common, cases were brought to light in which, though the male nuclei entered the oogonium, the nuclear fusion at that stage was omitted[2], the only fusion in the life history being that in the ascus. In such cases the fusion nucleus of the ascus is diploid, the four nuclei present after meiosis are haploid, and brachymeiosis does not occur. A transition condition has been found in *Pyronema domesticum*[3], where the ascogenous hyphae have begun to form before the male nuclei enter the oogonium, and where, as soon as
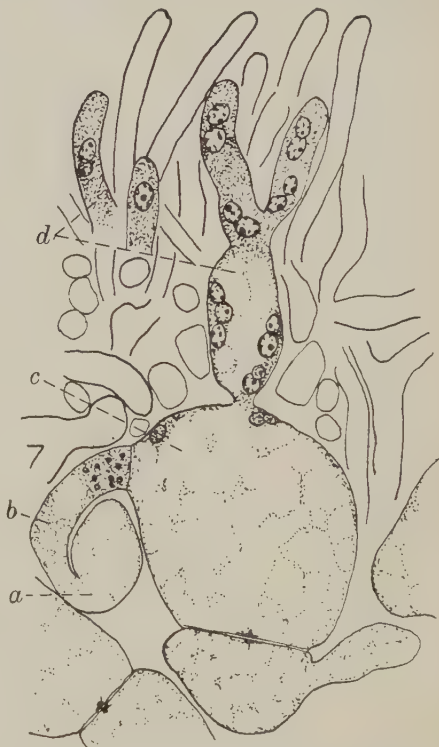
Fig. 81. *Pyronema confluens*; sexual apparatus and paired nuclei in the ascogenous hyphae; a, antheridium; b, trichogyne; c, oogonium; d, ascogenous hyphae; × 1040; after Claussen.

entrance has taken place, some of the sexual nuclei pass into the ascogenous hyphae without fusion, while others remain massed in the centre of the oogonium and fuse in pairs. Some of the ascogenous hyphae accordingly show haploid nuclei, and there is only one reduction in their asci, while, in other cases, the nuclei of the sporophyte are diploid, and two reductions in the ascus occur.

[1] Harper, 1905.   [2] Claussen, 1912; Ramlow, 1914.   [3] Tandy, 1927.

It has often been suggested[1] that, if the male and female nuclei do not fuse in the oogonium, they may travel side by side up the ascogenous hyphae, and the nuclei which fuse in the ascus may be respectively male and female in origin. Colour has been given to this view by the fact that, in any rapidly growing multinucleate hypha, nuclei are often found to be arranged in pairs (figs. 81, 82);

Fig. 82. *Ascophanus carneus* Pers.; germinating spores with paired nuclei in the germ tubes, × 450; after Ramlow.

the pairs in the ascogenous filaments were assumed to differ from those in vegetative hyphae in that the nuclei had become associated in the oogonium, and were respectively male and female. This hypothesis is not susceptible of proof, in that male and female nuclei cannot be recognised as such; it assumes the existence of a force sufficient to hold two nuclei together throughout growth and division in a multinucleate hypha. The case in the rusts is not comparable, for there the nuclei of the synkaryon are isolated from

[1] Raciborski, 1896; Claussen, 1912.

the beginning, two in each cell, and no attraction between them
need be presumed.

Apogamy. Apart from the failure of the sexual nuclei to fuse in
the oogonium, another degenerative process is in progress among the
Ascomycetes; in many the antheridium is missing, though the oogo-
nium still gives rise to ascogenous hyphae; in a much greater number
both organs have disappeared. Where an oogonium survives, its
nuclei may fuse in pairs before passing into the ascogenous hyphae;
where there are no sexual organs, union may take place between
the nuclei of vegetative cells, sometimes after the migration of a
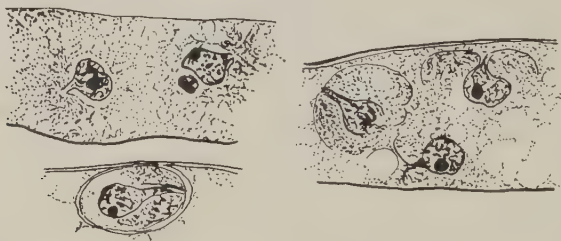
Fig. 83. *Humaria rutilans* (Fr.) Sacc.; stages of spore formation, × 1875.

nucleus from one cell to another. The cells in which fusion has
occurred give rise to ascogenous filaments; the condition is exactly
comparable with that in the prothallus of a pseudapogamous fern.
Finally there are cases where, the sexual organs being absent, and
no pseudapogamous fusion taking place, the nuclei of the asco-
genous hyphae are haploid and the only fusion is that in the ascus.
Owing to the existence of this fusion, meiosis survives when all
other trace of sexuality is lost.

Spore Formation. After the third division in the ascus pre-
parations for spore formation begin[1]. Each nucleus forms a beak
(fig. 83), at the tip of which is the centrosome and from which
the radiations of the aster spread into the cytoplasm. These radia-
tions doubtless indicate the paths of altered substances emanating
from the centrosome as a centre of activity, and flowing back past
the nucleus as the beak pushes through the cytoplasm. As these
substances increase a membrane is formed and the spore, or the

[1] Faull, 1905; Harper, 1905; Fraser and Welsford, 1908; Fraser and Brooks,
1909.

end of it nearest the centrosome, is cut out; in the delimitation of the region remote from the centrosome the vacuoles of the cytoplasm take part. In some species delimitation is mainly due to the vacuoles; in others it depends principally on the astral rays.

Phylogeny. The specialised character of the ascus justifies a strong presumption in favour of the monophyletic origin of the Ascomycetes; speculation as to their possible ancestry has followed two main lines; they have been regarded as derived either from the Phycomycetes[1], or from the red algae or the ancestors of the latter[2]. There is an interesting resemblance to be traced between the sporogenous filaments and carpospore fructifications of the Florideae and the ascogenous hyphae and ascocarps of the Ascomycetes, and also between the male and female organs of the two groups; but any suggestion of relationship between them is concerned with the higher Ascomycetes and involves the assumption that the simpler forms are reduced from the more complex.

The structure of these simpler forms constitutes a similar objection to the derivation of the Ascomycetes from any but the more primitive of existing Phycomycetes, though the evolution of the conidium both in the Peronosporaceae and in the Choanephoraceae and Mortierellaceae suggests a possible origin for the accessory spores, and the sexual apparatus of *Syncephalastrum* offers at least an example of parallel development. There is not, however, sufficient evidence to exclude the possibility of a separate flagellate ancestry, and effective speculation as to the origin of the Ascomycetes must await knowledge of the development of a larger number of forms.

Within the group it seems probable that the most primitive species are to be sought among the relatively simple forms included in the Plectascales. In most of the Endomycetaceae the oogonium becomes the ascus directly, so that there are no ascogenous hyphae and the first nuclear divisions after fertilisation bring about reduction. Members of the family showing slight development of ascogenous hyphae have recently been discovered. It is possible that we have here the origin of the vegetating sporophyte of the Ascomycetes; the neighbouring family, Gymnoascaceae, with its loose network of protective hyphae around the asci, certainly sug-

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[1] Atkinson, 1915.
[2] Dodge, 1914.

gests the origin of the peridium. Attempts at a natural classification, however, are limited by the scarcity of detailed knowledge, so that the efficient study of additional forms is greatly to be desired.

The Ascomycetes may be subdivided as follows:

Ascocarp, if present, either with no definite ostiole, or shield-shaped, or with asci irregularly arranged	PLECTOMYCETES
Ascocarp wide open when ripe; asci in parallel series	DISCOMYCETES
Ascocarp flask-shaped when ripe; asci in parallel series	PYRENOMYCETES

PLECTOMYCETES

The Plectomycetes[1] include those relatively simple forms which possess neither the cup-shaped apothecium of the Discomycetes nor the flask-shaped perithecium of the Pyrenomycetes. In most of the species a rounded ascocarp is produced, opening either by the decay of its wall, or by an irregular tear or split. The asci may arise from the floor of this fructification and stand parallel one to another, or they may be irregularly disposed, the fertile hyphae forming a tangled weft. In other cases a definite fructification is lacking.

The asci are usually pyriform, club-shaped or ovoid, in contrast to the nearly cylindrical asci of most of the Discomycetes and Pyrenomycetes. They arise indifferently from terminal or intercalary cells of the ascogenous hyphae. Except in the Perisporiaceae, the ascospores are usually continuous and hyaline. In most species the gametophytic mycelium gives rise to conidia.

The sexual apparatus is simple, and the oogonium after fertilisation may become an ascus directly, or may give rise to ascogenous hyphae.

The Plectomycetes include some 1200 species and may be subdivided as follows:

Asci irregularly arranged	PLECTASCALES
Asci parallel	
Ascocarp present	ERYSIPHALES
Ascocarp lacking	EXOASCALES

[1] Gwynne-Vaughan, 1922.

PLECTASCALES

The Plectascales include all those Ascomycetes in which the asci are irregularly arranged. In the simplest forms the asci are produced singly, one from each oogonium, and are without protective filaments; in *Gymnoascus* and its allies ascogenous hyphae are formed after fertilisation, and they, and the asci which they bear, are surrounded by an open weft of thick-walled hyphae; in the higher families a well-developed ascocarp is present.

The alliance includes the following families:

Asci naked

<div style="margin-left:2em">

Cells forming a mycelium; asci distinct from
  mycelial cells   ENDOMYCETACEAE
Cells single or loosely attached; asci not
  differentiated from other cells   SACCHAROMYCETACEAE
</div>

Asci surrounded by loosely interwoven hyphae   GYMNOASCACEAE

Asci surrounded by a definite peridium

<div style="margin-left:2em">

Ascocarp subaerial
  Sessile   ASPERGILLACEAE
  Stalked   ONYGENACEAE
Ascocarp subterranean

Peridium distinct from contents of ascocarp;
  spore mass powdery at maturity   ELAPHOMYCETACEAE
Peridium continuous with contents of ascocarp;
  spore mass never powdery   TERFEZIACEAE
</div>

ENDOMYCETACEAE

In the Endomycetaceae[1] the mycelium is extensive and bears numerous asci each of which is either the product of a separate, sexual fusion, or is parthenogenetically developed. Oidia, chlamydospores, and yeast-like conidia may be formed. Most of the Endomycetaceae are saprophytic on sugary substances or on exudations from plants; *Endomyces Mali* is described as an active parasite on apples, some other species are parasitic on fungi, and *Endomyces albicans* is now recognised as a cause of the human disease known as thrush. The principal genera of the family are *Eremascus* and *Endomyces*.

Only two species of *Eremascus* are known. *E. albus*[2] was discovered by Eidam in 1881, in a bottle of malt extract. The con-

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[1] Klöcker, 1909 i; van der Wolk, 1913; Ramsbottom, 1914; Juel, 1921; Mangenot, 1922.
[2] Eidam, 1883.

tents had gone bad and were covered with a growth of fungi, among which was the new form. It produced a fine, snowy white, septate mycelium from which pairs of fertile hyphae grew out, curled round one another, and fused at their tips (fig. 84). The fused portion was cut off by a wall and eventually produced eight spores. Unfortunately the species was lost and has never reappeared.
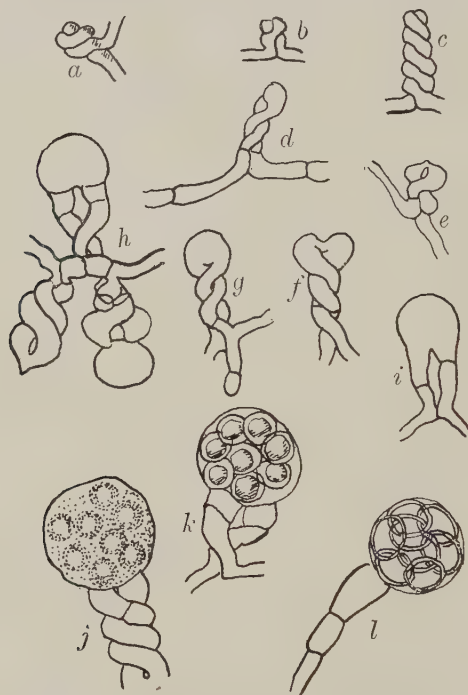
Fig. 84. *Eremascus albus* Eidam; *a, b, c, d*, sexual apparatus; *e, f, g, h*, fusion of gametangia; *i, j, k*, development of asci; *l*, parthenogenetic ascus; × 900–1000; after Eidam.

In 1907, however, Stoppel, on opening some pots of currant and apple jelly, discovered a similar form which she named *Eremascus fertilis*. This species[1], like *E. albus*, possesses a branching, septate mycelium. Pairs of uninucleate cells grow up from the same or different hyphae; they unite (fig. 85), their nuclei fuse, and after three karyokinetic divisions eight spores are formed. Sometimes, especially in old cultures, the fertile hyphae may produce

[1] Stoppel, 1907; Guilliermond, 1909.

asci without fusion; these are usually smaller than the ordinary asci and contain four or fewer spores.

The species of *Endomyces*[1] possess a branched, septate mycelium. This may break up into oidia, which sometimes become surrounded by thick walls and form cysts, or may produce yeast-like conidia which themselves multiply by budding. The mycelium also bears naked, four-spored asci, the spores of which are often of a characteristic bowler-hat shape.
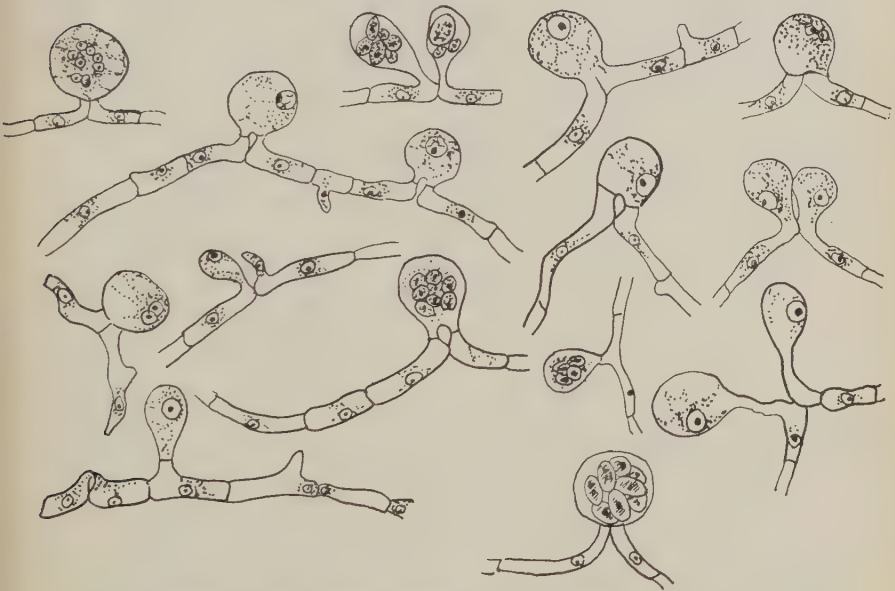
Fig. 85. *Eremascus fertilis* Stoppel; stages in the formation of the ascus, both by fusion of two cells and parthenogenetically; after Guilliermond.

In *Endomyces Magnusii* vegetative multiplication is by oidia, cut off by transverse walls. The ascus is the product of a sexual process in which an elongated, swollen cell and a relatively narrow cell bend towards one another and unite. The single nucleus of the smaller cell passes into the larger and fuses with its nucleus; the fusion nucleus divides twice, and four spores are formed (fig. 86). Fusion appears to take place indifferently between related or unrelated filaments, and parthenogenesis is not uncommon.

In *E. fibuliger* about half the asci result from the union of two

[1] Guilliermond, 1909, 1913; Juel, 1921.

filaments while the remainder are parthenogenetic. The fusing
hyphae are in most cases related; both are similar at the time of
fusion, but afterwards the growth of one ceases and the other swells
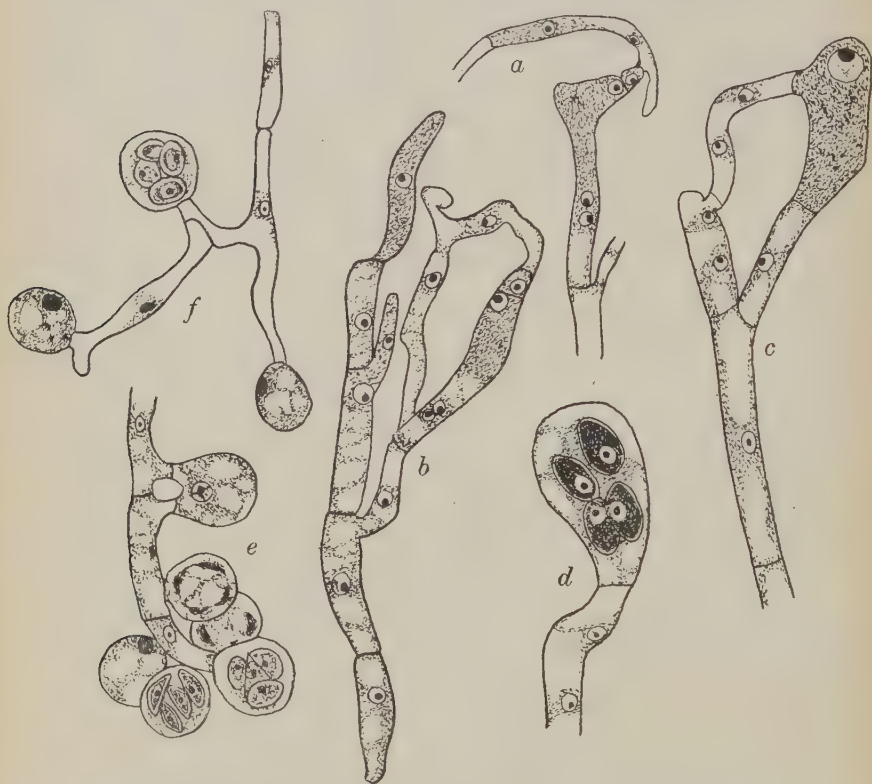
Fig. 86. *Endomyces Magnusii* Ludw.; *a, b*, antheridium and oogonium in con-
tact; *c*, oogonium after fusion of sexual nuclei; *d*, parthenogenetic ascus.
Endomyces fibuliger Lindner; *e*, conjugation between two neighbouring cells,
at the end of the hypha is a group of young asci; *f*, normal and parthenogenetic
asci; after Guilliermond.

to form the ascus. Vegetative multiplication (fig. 87) is by yeast-
like conidia.

E. *Lindneri*[1] resembles E. *fibuliger* in its vegetative characters,
but the gametangium, instead of functioning as an ascus, sometimes
gives rise to short branches bearing two or more asci (fig. 88).

[1] Mangenot, 1919.

These may be regarded as constituting a brief sporophytic stage and as corresponding to the ascogenous hyphae of higher forms.

Fig. 88. *Endomyces Lindneri* (Saïto) Mang.; two asci on short ascogenous hyphae developed from a pair of fused gametangia; after Mangenot.

Fig. 87. *Endomyces fibuliger* Lindner; formation of conidia; after Guilliermond.
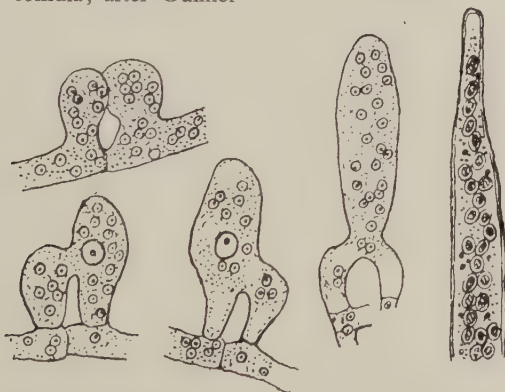
Fig. 89. *Dipodascus albidus* Lagerh.; development of ascus and ascospores; after Juel.

Parthenogenesis, however, is common, and nuclear fusion has not yet been seen.

Dipodascus[1] (fig. 89) differs from other Endomycetaceae in the presence of accessory nuclei in its gametangia, and in the forma-

[1] de Lagerheim, 1892; Juel, 1902, 1921; Dangeard, 1907.

tion of numerous spores in its ascus. In the initiation of the ascus two branches grow up from the same or different hyphae and fuse at their tips; one is larger than the other and continues its growth after fertilisation to form the single ascus. Soon after the fusion of the gametangia one of the nuclei in each is seen to be larger than its neighbours; while the remainder of the nuclei degenerate, these two unite, and, after several divisions, give rise to the nuclei of the spores.

SACCHAROMYCETACEAE

The Saccharomycetaceae, or yeasts[1], appear mainly as separate cells, which are only exceptionally united to form a mycelium; they are widely distributed in or on sugary media, and some are found as parasites in plants and animals, including man. As a rule they do little damage, those in healthy animals being soon destroyed by leucocytes, but in *Monospora bicuspidata*[2] the needle-like ascospores penetrate the gut wall of *Daphnia*, multiply by budding, and may bring about the death of the host, while the presence of *Nematospora*[3] may kill or injure the seeds of legumes.

The individual cell is round or elliptical, bounded by a delicate membrane and possessing a relatively large nucleus with which is associated a vacuole containing metachromatic granules. Division is usually of a simple type, but karyokinesis occurs in the cells of *Schizosaccharomyces octosporus*[4], *Nematospora Phaseoli*[5] and other species. In the cytoplasm are refractive granules of volutin, glycogen and oil.

Multiplication is by transverse division and separation of the daughter cells, as, for instance, in *Schizosaccharomyces*, or, more usually, by budding, that is to say, by the formation of successive outgrowths which attain the form and size of the parent cell; each bud receives a nucleus and cytoplasm and is cut off by a wall; before its separation it may bud again, and in this way considerable colonies are formed. Budding occurs in *Saccharomyces*, *Zygosaccharomyces* and *Saccharomycopsis*. Under suitable conditions, and especially when growing on a moist, solid substratum, the cell

[1] Guilliermond, 1901, 1903, 1905 ii, 1910 i, ii, 1920 i, ii; Hansen, 1901; Klöcker, 1909 ii; Nadson and Konokotine, 1910; Wager and Peniston, 1910; Marchand, 1913; Satava, 1918; Guilliermond and Péju, 1920.
[2] Keilin, 1921.   [3] Wingard, 1922, 1925.
[4] Guilliermond, 1920 ii.   [5] Wingard, 1925.

contents may round themselves up and form one to eight spores, produced, in some cases at least, by free cell formation. These so-called **endospores** are the ascospores of the yeast, the vegetative cell functioning as an ascus, either independently, or after conjugation with a similar cell.

One of the most striking features of the yeasts, which gives them considerable economic importance, is the power possessed by many species of producing alcoholic fermentation in solutions of suitable sugars[1]; under conditions of plentiful aeration the yeast grows and multiplies rapidly, and much of the sugar is used as food; when free oxygen is insufficient, the main part of the sugar
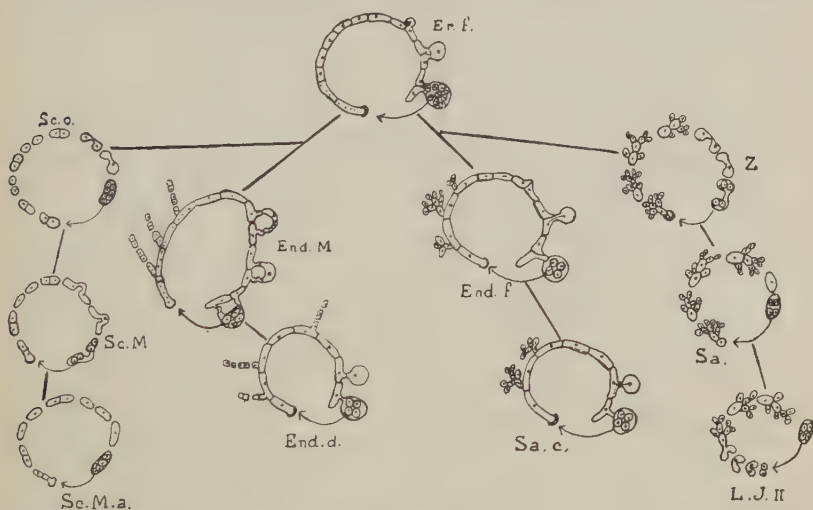
Fig. 90. Diagram of the phylogeny of the Yeasts; after Guilliermond. Er. f., *Eremascus fertilis*. End. f., *Endomyces fibuliger*. Sa. c., *Saccharomycopsis capsularis*. Z., *Zygosaccharomyces*. Sa., *Saccharomyces*. L. J. II, Johannisberg yeast II. End. M., *Endomyces Magnusii*. End. d., *Endomyces decipiens*. Sc. o., *Schizosaccharomyces octosporus*. Sc. M., *Schizosaccharomyces mellacei*. Sc. M. a., *Sch. mellacei*, apogamous variety.

is utilised in respiration, alcoholic fermentation is more complete, and the quantity of alcohol produced is greater in proportion to the number of cells concerned.

On the ground that their daughter cells are produced by septation, and not, as in other genera, by budding, Guilliermond[2] (fig. 90) has postulated for the species of *Schizosaccharomyces* a derivation

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[1] Cf. p. 18.   [2] Guilliermond, 1909.

from the neighbourhood of *Endomyces Magnusii*; he refers the genera, such as *Saccharomyces*, in which budding occurs, to the line which gave rise to *E. fibuliger*. In both cases the yeasts are regarded as reduced from the filamentous Endomycetaceae.

Conjugation as a preliminary to the formation of asci has been observed in a number of species[1]. In *Schizosaccharomyces octosporus* (fig. 91) two neighbouring cells of similar size put out processes which fuse to form a conjugation tube; the nuclei pass into the tube and undergo fusion, after which the two associated cells enlarge and form a single, oval ascus; the nucleus meantime divides and four or eight ascospores are organised about the daughter nuclei. In *Zygosaccharomyces Barkeri* a similar process occurs, but the union of the conjugating cells is less complete, and the
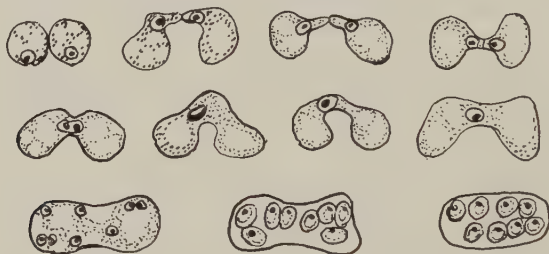
Fig. 91. *Schizosaccharomyces octosporus* Beyerinck; conjugation and formation of ascospores; after Guilliermond.

number of ascospores is regularly four. The family shows all stages of transition from such unions of morphologically and physiologically similar cells to the passage of the contents of a small cell into a large one, and even of the contents of a bud back into the parent cell.

In most species with sexually formed asci parthenogenesis is common; in *Schwanniomyces*[2] and *Torulaspora*[3] it has become the rule; the cells in which ascospores are about to be formed put out processes towards neighbouring cells, but they do not fuse, and ascospores are formed in each independently. Such cases lead up to the condition found in the majority of the yeasts where ascospore formation takes place, not only without effective conjugation, but without any vestige of that process.

[1] Schiönning, 1895; Barker, 1901; Guilliermond, 1901.
[2] Guilliermond, 1910 ii.   [3] Rose, 1910.

GYMNOASCACEAE

The Gymnoascaceae differ from the Endomycetaceae in that their asci are borne on a well-developed sporophytic mycelium which originates from one of the gametangia after the fertilisation stage. Further, these ascogenous hyphae are surrounded by a loose weft of protective filaments bearing spines or coiled or hooked branches (fig. 92). The asci are ovoid or pyriform and each contains eight spores.

The species of *Gymno-ascus* occur as saprophytes on dung, dead grass, bees' nests, and other habitats. In *G. Reessii*[1] two branches grow up from the same hypha, one on each side of a septum, and become twisted round one another. Their free ends swell and are cut off by transverse septa forming the gamet-angia; the walls between them break down, the con-tents of the antheridium pass into the oogonium

Fig. 92. *Gymnoascus* sp.; *a*, ascocarp, × 265; *b*, ascus and free ascospores, × 1040.

(fig. 93 *a*, *b*), and the oogonium puts out a branch which under-goes septation and gives rise to the ascogenous hyphae. The sexual organs are at first uninucleate but later coenocytic; the fusion of the nuclei has not been recognised. In *G. candidus*[1] (fig. 93 *d*), the gametangia usually arise from different hyphae; they differ in form at the time of their union, the antheridium is straight and somewhat swollen, the oogonium grows spirally round it till the apices meet and fuse (fig. 93 *e*); afterwards the oogonium undergoes septation and gives rise to ascogenous hyphae; the sheath of protective filaments is very scanty.

Ctenomyces serratus[2] (fig. 93 *f*), which occurs saprophytically on

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[1] Dale, 1903.   [2] Eidam, 1880; Marsh, 1926.

feathers and other *débris*, and *Amauroascus verrucosus*[1], on leather, form sexual organs which, in the early stages, closely resemble those of *Gymnoascus*. In *Amauroascus*, however, the oogonium is stated to give rise to ascogenous hyphae without septation.

Several of the fungi responsible for skin diseases[2] have been shown to be degenerate members of this family; traces of the characteristic outgrowths from the weft of hyphae which surrounds the asci of normal forms are still found on the mycelium.

Fig. 93. *Gymnoascus Reessii* Baran.; *a*, surface view of conjugating cells; *b*, the same in longitudinal section; *c*, a later stage, septate branch from oogonium giving rise to ascogenous hyphae. *Gymnoascus candidus* Eidam; *d*, surface view of conjugating cells; *e*, same in longitudinal section; all after Dale. *Ctenomyces serratus* Eidam; *f*, surface view of conjugating cells, × 400; after Eidam.

ASPERGILLACEAE

The Aspergillaceae[3] are distinguished from the earlier families of the Plectascales by the fact that their ascogenous hyphae are surrounded by a continuous sheath of gametophytic filaments, so that a closed fruit, or perithecium, is formed. In many species the development of ascocarps in nature is rare, and multiplication depends on the abundant conidia; in others which, judging from their conidial fructifications, belong to this family, ascocarps are unknown.

The species occur on a wide variety of substrata; some of them,

[1] Dangeard, 1907.   [2] Grigoraki, 1925.
[3] Thom and Church, 1926.

if they obtain entrance through a wound or other aperture, are the cause of ripe rot in fruit. *Thielavia basicola*, however, is the only member of the family which causes an important plant disease; it infects the roots of tobacco and other angiosperms, and, in the early stages, multiplies by means of hyaline conidia. These are developed[1] from somewhat bulbous conidiophores with the walls of which their own walls are at first continuous; the rupture of the wall sets the conidia free in acropetal succession. Later, rows of thick-walled brown chlamydospores are differentiated. Normal development of the infected root is prevented and the host is killed or stunted; if death ensues, perithecia develop on the dead plant.

The formation of a perithecium in the Aspergillaceae is initiated by the appearance of sexual organs, from the stalks of which the cells of the sheath arise. In *Microascus* and *Emericella* the sheath opens by a pore, in other cases it remains closed, and the ascospores are liberated by its decay. The asci are spherical or pyriform and contain two to eight spores. Both in *Penicillium* and *Eurotium* sclerotia sometimes appear which resemble the perithecia, but possess an exceptionally thick wall and contain no asci; they may prove to be immature perithecia which have passed into a resting state.

In the investigated species of *Eurotium* the cells of the mycelium are multinucleate; conidiophores appear early, as thick aseptate hyphae, the free end becomes swollen and buds out numerous sterigmata (fig. 94), from each of which conidia are formed in acropetal succession; nuclei stream up the strands of cytoplasm into the sterigmata and thence to the developing conidia. At maturity each conidium in *E. repens* contains twelve nuclei, in *E. herbariorum* four, and in some of the rarer species only one.

The archicarp of *Eurotium herbariorum*[2] is made up of three parts, a multicellular stalk, a unicellular oogonium and a unicellular trichogyne. It becomes more or less twisted (fig. 95 *a*) and near it another septate hypha appears from the end of which the unicellular antheridium is cut off. Like the cells of the mycelium all parts of the sexual apparatus are coenocytic. Fusion takes place between the antheridium and trichogyne, but the contents of the male organ have not been seen to enter the oogonium.

[1] Brierley, 1915.   [2] de Bary, 1870; Fraser and Chambers, 1907.

Fig. 94. *Eurotium herbariorum* (Wigg.) Link; development of conidiophores and conidia, × 625.

Fig. 95. *Eurotium herbariorum* (Wigg.) Link; *a*, young archicarp; *b*, archicarp and abortive antheridium; *c*, ascocarp containing asci and spores; × 625.

Both in *E. repens*[1] and *E. Fischeri*[2] fusions of nuclei in the oogonium have been recorded, but they are probably fusions of female nuclei in pairs, and not of male and female nuclei. Even if normal

Fig. 96. *Penicillium glaucum* Link; conidiophores and conidia, × 500.

fertilisation still sometimes occurs, it is certainly not general, for the antheridium often fails to reach the trichogyne (fig. 95 *b*) and is sometimes absent altogether.

Nevertheless the oogonium becomes septate and from its cells branches develop, and give rise to asci. The ascus is formed from the terminal or penultimate cell of a hypha and in it fusion of two nuclei takes place. The spores have a sculptured epispore and are

[1] Dale, 1909.   [2] Domaradsky, 1908.

of very characteristic form, so that, when seen laterally, they some-
what resemble a butcher's tray (fig. 95 c).

Shortly before the septation of the oogonium vegetative hyphae
begin to grow up about the sexual
organs; some of them extend inwards
forming a nutritive layer, while others
constitute the outer wall of the sheath
and secrete a thick, brittle pellicle
of golden yellow substance, readily
soluble in alcohol. Later the asco-
genous hyphae, the nutritive cells,
and the walls of the asci are
absorbed, supplying food to the

Fig. 97. *Penicillium glaucum*
Link; conjugating cells, × 630;
after Brefeld.

developing spores, and the spores at last lie free within the outer
layers of the sheath and are liberated by its decay. *Eurotium* was

Fig. 98. *Monascus Barkeri* Dang.; development of oogonium, trichogyne
and antheridium, × 900; after Barker.

known for some time before its perithecia and conidia were
recognised as belonging to the same form; the generic name

Aspergillus was given to the conidial stage and still survives in the name of the family.

In most species of *Penicillium*[1] multiplication takes place chiefly by means of the abundant conidia borne in chains on branched, brush-like conidiophores (fig. 96). Ascocarps are rare, and a
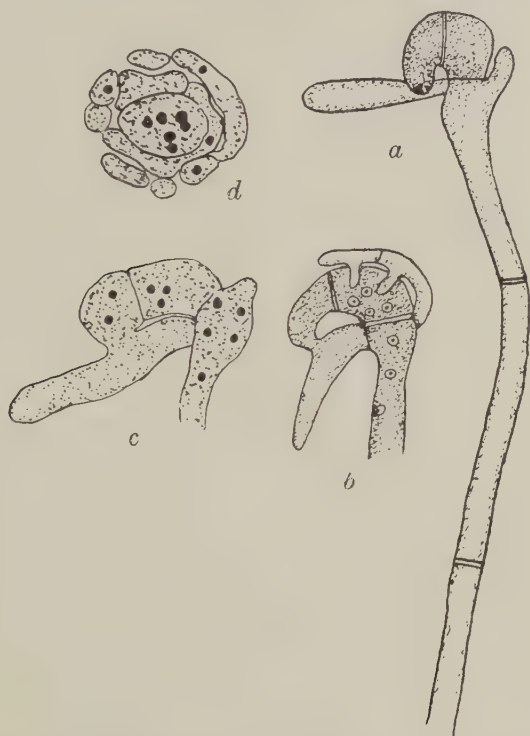
Fig. 99. *Monascus purpureus* Went.; *a, b*, stages in the development of the oogonium; after Dangeard. *Monascus X*. Schikorra; *c*, entrance of male nuclei into trichogyne; *d*, pairing of nuclei in the oogonium; after Schikorra.

detailed study of their development has yet to be made. They have been obtained from time to time by growing the fungus under reduced atmospheric pressure, by excluding air, or by cultivation on concentrated sugar solution. Their formation is initiated by the appearance of pairs of stout, twisted hyphae (fig. 97), one of which is probably the archicarp. A further study

[1] Brefeld, 1874; Zukal, 1887; Klöcker, 1903; Dangeard, 1907; Thom, 1910; Bezssonof, 1918 i.

of these structures is much to be desired, especially in view of their resemblance to the gametangia of *Gymnoascus*.

In the genus *Monascus*[1] there is an abundant mycelium bearing chains of ovoid conidia. *M. Barkeri* is used by the Chinese for the manufacture of an alcoholic liquor known as Samsu. Both in this species and in *M. purpureus* the development of the sexual organs can be observed with some readiness in a hanging drop. Certain branches of the mycelium cut off a small terminal cell which elongates and bends sideways to form the antheridium (fig. 98). A prolongation of the penultimate cell grows alongside it and divides into two; these are the trichogyne and oogonium. The oogonium contains four to six nuclei and the antheridium three or four. Fusion takes place between the antheridium and trichogyne, and the male nuclei travel through the trichogyne to the oogonium where they pair with the female nuclei (fig. 99). The oogonium enlarges and gives rise, apparently without septation, to ascogenous hyphae,

Fig. 100. *Terfezia olbiensis* Tul.; section of fructification; after Tulasne.

while the antheridium and trichogyne degenerate. Investing filaments grow up to form a sheath within which the ascospores are finally set free. The sheath with its contained spores was long regarded as a single large ascus, and to this misapprehension the name *Monascus* is due.

ONYGENACEAE

The Onygenaceae include only the remarkable genus *Onygena*[2], characterised by the limitation of its species to such habitats as horns, hooves, fur and feathers; by the absence of conidia; and by the thin wall of the perithecium, which opens by lobes or by a circular split. The best known species is *Onygena equina*, in which the ascocarp first appears as a dome-shaped mass of white hyphae;

[1] Barker, 1903; Ikeno, 1903 ii; Kuyper, 1905; Olive, 1905; Schikorra, 1909.
[2] Ward, 1899; Brierley, 1917.

the outer of these divide into short segments which are liberated as chlamydospores. Asci are produced internally and give rise to eight spores each; the ascus walls soon disappear and the ascospores lie free among the vegetative hyphae. This mature stage,
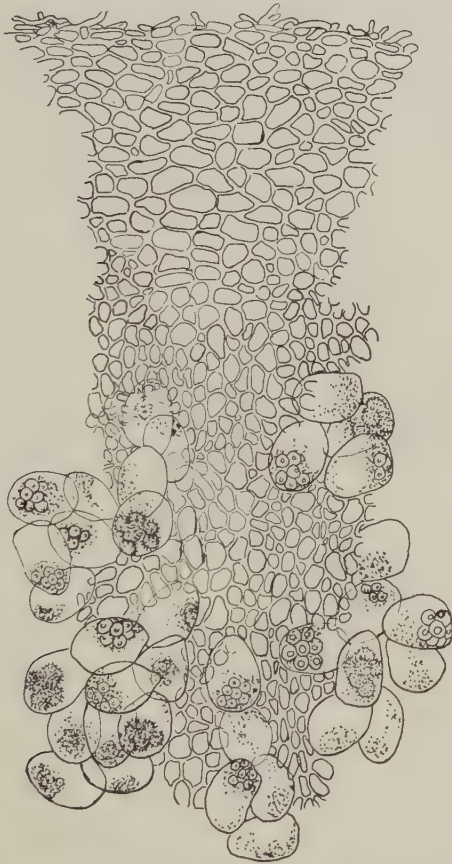
Fig. 101. *Terfezia olbiensis* Tul.; section through hymenium, showing asci irregularly arranged; after Tulasne.

in which there is no trace of asci, caused *Onygena* to be classified with the Myxomycetes and also with the Lycoperdaceae before its true position was discovered. There is no sign of sexual organs.

ELAPHOMYCETACEAE AND TERFEZIACEAE

In these two families the fruit is subterranean; it differs from that of other hypogeal Ascomycetes, and resembles that of the sub-aerial Plectascales in the irregular arrangement of the asci, which are scattered or grouped in nests surrounded by sterile branches; the fertile tissue is not exposed at any stage of development.

In the Elaphomycetaceae the ascocarp is surrounded by a thick, yellow or brown peridium, the asci are subglobose, and the interior of the perithecium is filled at maturity by a powdery mass of spores. The only genus is *Elaphomyces*. The mycelium develops in relation to the roots of conifers, and the ascocarp is often parasitised by the pyrenomycetous fungus *Cordyceps*[1]; *E. granulatus*, the commonest British species, is the host of *C. capitata*, and *E. variegatus* of *C. ophioglossoides* (fig. 164).

In the Terfeziaceae (figs. 100, 101) the peridium is less distinct, and in some cases is represented merely by an ascus-free region in the periphery of the fruit. The spores do not, as in *Elaphomyces*, form a powdery mass at maturity.

ERYSIPHALES

The Erysiphales are characterised by an abundant, superficial mycelium which may be colourless or dark-coloured. The perithecia are spherical, ovoid or flattened, and are usually without an ostiole; the peridium is thin and membranous; the asci are parallel one to another, forming a regular layer at the base of the fructification.

The alliance includes some 600 species, most of which are epiphytes or external parasites on the leaves of higher plants, and which may be classified as follows:

Aerial mycelium colourless. Perithecia more or less globose without an ostiole, furnished with conspicuous appendages. Conidia in single rows	ERYSIPHACEAE
Aerial mycelium dark in colour, rarely absent. Perithecia globose or ovoid, without appendages. Conidia not in single rows	PERISPORIACEAE
Aerial mycelium dark in colour or absent. Perithecia flattened or shield-shaped, with an ostiole, without appendages. Conidia absent	MICROTHYRIACEAE

[1] Cf. p. 215.

The Erysiphaceae alone have received detailed study. They are apparently a primitive family and approach the Plectascales in the characters of their sexual organs, in their type of perithecium, and especially in their globose asci with colourless, continuous spores. In the Perisporiaceae, on the other hand, the spores are commonly two or more celled and often dark-coloured, the asci are usually cylindrical, as in the Pyrenomycetes, and some of the characters of the perithecium also recall the lower members of that group. The Microthyriaceae approach the Perisporiaceae in the characters of the ascus and spore, but are clearly distinguished by their curious, flattened perithecium.

ERYSIPHACEAE

The members of the Erysiphaceae[1] are popularly known as white or powdery mildew or blight. Their distribution is almost cosmopolitan, and they have been recorded especially in Europe and North America.

They are obligate parasites on the leaves, young shoots and inflorescences of flowering plants. Both the conidium and the ascospore give rise on germination to an abundant, superficial mycelium of uninucleate cells, which forms a white, web-like coating over the leaf and sends haustoria into the epidermal cells of the host. In the simplest examples the haustorium is a slender tube which swells inside the host cell; in other cases it is branched, sometimes forming finger-like processes, and frequently provided with an external disc or appressorium, from which, or from the mycelium in the neighbourhood of which, the haustorium proper arises and pushes into the epidermal cell. As a rule the fungus does not penetrate further, but in *Erysiphe Graminis* endophytic growth is induced if the conidia germinate on wounded leaves; in *Phyllactinia Corylea* the branches of the aerial mycelium enter through the stomata, extend through the intercellular spaces and send haustoria into the neighbouring cells; and in *Erysiphe taurica* the whole mycelium during the conidial stage is located in the tissues[2]. When perithecia are about to be produced the mycelium emerges and spreads over the surface of the host; both in *Phyllactinia* and in *E. taurica* the aerial hyphae show appressoria although no haustoria are formed. It may be inferred that they are derived

[1] Salmon, 1900–7; Sands, 1907.   [2] Salmon, 1905–6.

from forms which possessed a purely subaerial mycelium with
haustoria, and that the ecto-
phytic condition is primitive
in the family. An alternative
descent from endophytic
Pyrenomycetes with stro-
mata in the tissues of the
host has, however, been
proposed[1].

The Erysiphaceae are
propagated in summer by
rather large, oval, uni-
nucleate conidia[2] (fig. 102),
produced in rows on un-
branched conidiophores.
Before the connection of
the conidial stage with the
perithecial was recognised

Fig. 102. *Sphaerotheca pannosa* Wallr.;
conidiophores and conidia, × 240.

the generic name *Oidium* was used for the former and it still
survives for species in which the perithecia have not been seen.

Fig. 103. *Erysiphe Polygoni*; young perithecium containing uninucleate
asci; after Harper.

The perithecia of the Erysiphaceae appear in the late summer
or autumn; they are spherical or sub-globose, 0·05 to 0·3 mm. in

[1] Arnaud, 1920.　　　　　　　　[2] Foëx, 1912.

diameter, and furnished with simple or branched appendages; they are fixed to the substratum by means of a secondary mycelium. When young the perithecia are white and glistening like the vegetative hyphae, later they become clear yellow, and finally brown
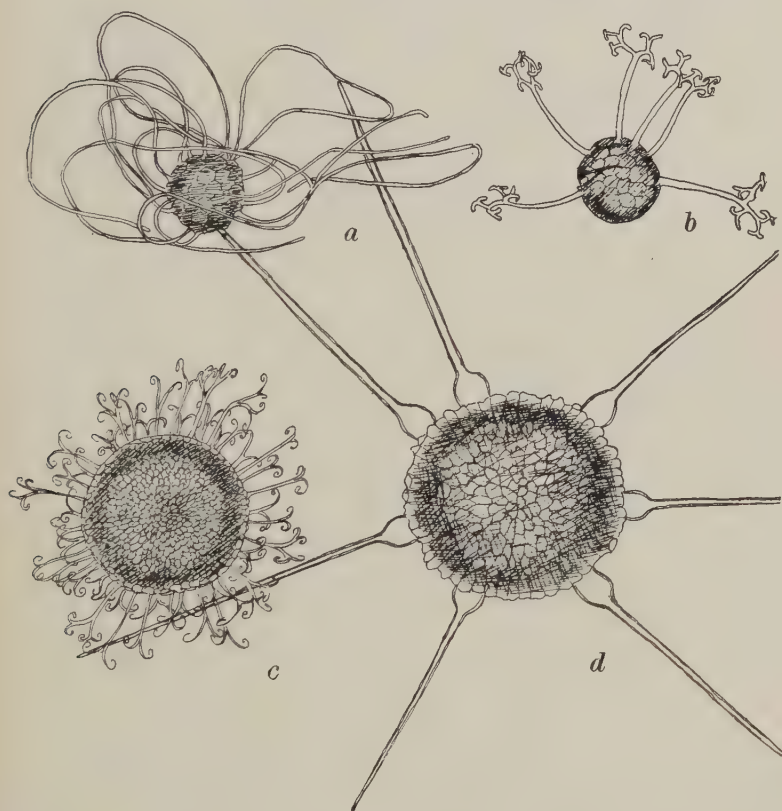
Fig. 104. Perithecia of *a*, *Erysiphe tortilis* (Wallr.) Fr.; *b*, *Microsphaera* sp.; *c*, *Uncinula Aceris* (DC.) Sacc.; *d*, *Phyllactinia Corylea* (Pers.) Karst.; × 120.

in colour; a considerable range of stages can often be seen within the field of a hand lens.

During development the wall of the perithecium is differentiated into inner and outer layers (fig. 103). The inner layer is made up of thin-walled cells rich in cytoplasm; it forms a packing round the developing asci and supplies them with food material. The function of the outer layer is protective; its cells have scanty con-

tents, and their walls undergo a change analogous to lignification; from this layer the characteristic appendages are derived.

A single ascus is formed in the perithecium of *Sphaerotheca* and *Podosphaera*; in other genera several asci are formed; the spores

Fig. 105. *Sphaerotheca Humuli* (DC.) Burr.; *a*, young oogonium and antheridial hypha; *b*, entrance of male nucleus; *c*, male and female nuclei in oogonium; *d*, fertilisation; *e*, fusion nucleus; *f*, nuclei produced by first division of fusion nucleus; *g*, young perithecium with binucleate ascogenous cell; × 1360; after Blackman and Fraser.

in each ascus number two to eight. The development of the spores begins in the summer or autumn[1], but they are not ordinarily set free by the decay of the perithecial wall until the following spring, when they produce the first infections of the season.

The perithecial appendages (fig. 104) are filamentous, un-

[1] Salmon, 1913 i, ii, iii.

branched or branched irregularly in *Sphaerotheca* and *Erysiphe*; in *Podosphaera* and *Microsphaera* they are dichotomously branched; in *Uncinula* their apices are spirally coiled; and in *Phyllactinia* the perithecia bear stiff, pointed hairs with swollen bases. In the last named genus the top of the young perithecium is furnished with a ring of short, richly branched hyphae. At about the time of spore formation these break down, forming a sticky, gelatinous cap by which the perithecium, when first set free, adheres upside down to its original host or to other objects. In view of this peculiarity *Phyllactinia* must not be ascribed, without verification, to any plant on which its perithecia happen to be found. The function of the appendages is in most cases to anchor the perithecium to the host during development, but in *Uncinula* the tips become mucilaginous and serve the same purpose as the branched cells of *Phyllactinia*. In *Phyllactinia* the bulb at the base of the appendage executes hygroscopic movements, its underside being pushed in and therefore shortened as water is lost; in this way, when the perithecium is ripe and ceases to absorb water, it is loosened from the host leaf.

The first account of development in this family, as in so many others, is due to de Bary, who described *Sphaerotheca Humuli* in 1863; his work has since been confirmed and extended[1]. This species occurs on a number of common plants, and is the cause of strawberry mildew and of the mildew on the hop. The sexual organs arise as lateral branches from the mycelium and project at right angles to the infected surface. The oogonium is an oval, uninucleate cell; it is cut off from the parent hypha and a stalk cell may be differentiated below it (fig. 105 *a*). The antheridium is much smaller and is borne on an elongated, narrow stalk (fig. 105 *c*); like the oogonium it contains a single nucleus. The wall between the oogonium and antheridium now breaks down, the male nucleus passes into the oogonium, and unites with the female nucleus (fig. 105 *d*); mitosis follows, and the oogonium is divided into a row of cells (fig. 105 *g*), the penultimate of which contains two nuclei and becomes the single ascus. Meanwhile a sheath of gametophytic hyphae has grown up around the sexual apparatus and forms the wall of the perithecium. Specimens have been

[1] de Bary, 1863 ii; Harper, 1895, 1897; Blackman and Fraser, 1905.

described in which the male nucleus fails to enter the oogonium (fig. 106), and it seems likely that apogamy is not uncommon[1].

Erysiphe Polygoni[2] occurs on the leaves and stems of a considerable variety of hosts. The development of the sexual organs and the union of the sexual nuclei (fig. 107 *a*) take place much as in *Sphaerotheca*, and, as in *Sphaerotheca*, the oogonium, after fertilisation, elongates and divides to form a row of cells, while gametophytic hyphae constitute a protective sheath. The penultimate cell of the row formed from the oogonium, however, usually contains more than two nuclei and, instead of becoming the ascus directly, it buds out ascogenous hyphae (fig. 107 *b*), at the ends of which a number of asci are formed.

Fig. 106. *Sphaerotheca Humuli* (DC.) Burr.; development of archicarp; in *c*, two nuclei, regarded as the product of division, are shown in the oogonium, while a cell at the top of the oogonium, regarded as the antheridium, still contains a nucleus; after Winge.

Phyllactinia Corylea[3] infects the leaves of deciduous trees and shrubs, including ash, oak, beech, hazel and hornbeam. The sexual organs arise where two hyphae meet; they become closely applied, and the oogonium, as it grows, sometimes becomes twisted around the antheridium. In due course the male nucleus enters the female organ (fig. 108 *a*), fusion takes place, the fusion nucleus divides, and a row of three to five cells is formed (fig. 108 *c*). The penultimate cell regularly contains more than one nucleus, the remainder are uninucleate. The sheath (fig. 109) arises from the stalk cells of the antheridium and oogonium. The ascogenous hyphae are formed as lateral branches from the septate oogonium; all or most being derived from the penultimate cell. Eight nuclei are formed as usual in each ascus, but spores are organised around only two.

[1] Dangeard, 1897, 1907; Winge, 1911; Bezssonof, 1914.
[2] Harper, 1896, 1905.   [3] Harper, 1905.
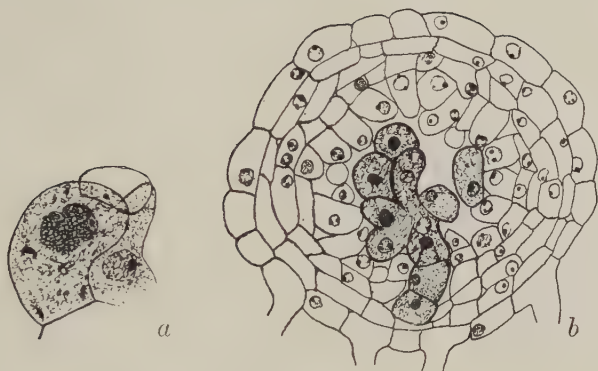
Fig. 107. *Erysiphe Polygoni*; *a*, fertilisation; *b*, young perithecium with ascogenous hyphae; after Harper.
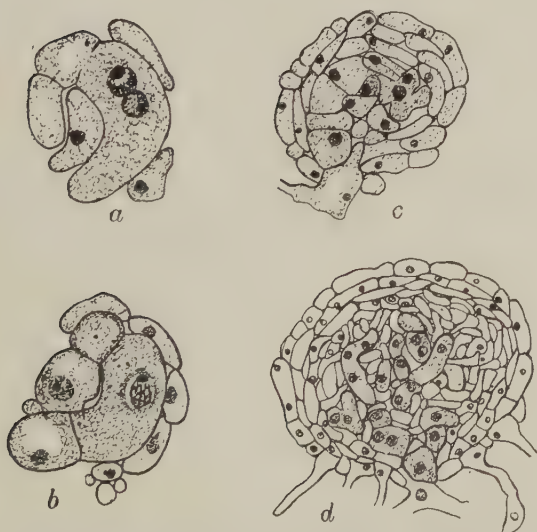
Fig. 108. *Phyllactinia Corylea* (Pers.) Karst.; *a*, fertilisation; *b*, fusion nucleus in oogonium; *c*, *d*, young perithecia; after Harper.
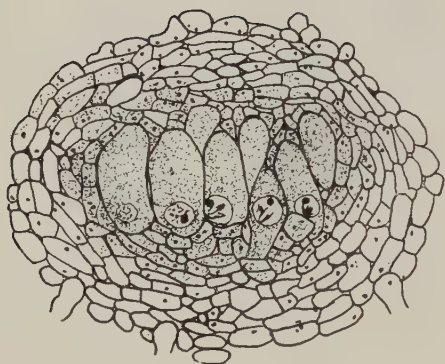
Fig. 109. *Phyllactinia Corylea* (Pers.) Karst.; perithecium containing uninucleate asci; after Harper.

Fig. 110. *Phyllactinia Corylea* (Pers.) Karst.; *a, b,* fusion in ascus; after Harper.

Fig. 111. *Phyllactinia Corylea* (Pers.) Karst.; *a,* metaphase of first division in ascus; *b,* anaphase of first division; *c,* anaphase of second division in ascus; *d,* anaphase of third division; after Harper.

In these and other investigated mildews the young ascus contains two nuclei; they fuse (fig. 110) and the fusion nucleus divides three times, the first two divisions (fig. 111) constituting a meiotic phase. The haploid number of chromosomes is eight in *Phyllactinia* and is stated to be four in species of *Sphaerotheca*[1].

Perisporiaceae

The Perisporiaceae include about 300 species, many of which are little known while none has been fully studied. They develop as epiphytes on the leaves or young parts of plants, or occur on decaying plant substances. The mycelium is dark-coloured and occasionally forms a stroma; in some cases no aerial mycelium is developed. The perithecia are always superficial and dark in colour; they are without appendages, though mycelial outgrowths from their base may simulate these structures as in *Meliola*. The spores may be liberated by the decay of the sheath, or there may be an irregular rent at the apex as in *Antennaria*, or the perithecium may open, as in *Capnodium*, by valves. The asci are elongated and more or less cylindrical, the spores have one or more septa and are sometimes muriform; paraphyses are not as a rule developed.

Dimerosporium, the largest genus, with some sixty species, is epiphytic on the leaves of Angiosperms; *D. Collinsii* forms witches' brooms on the service-berry.

The species of *Capnodium* and *Meliola* are among the soot fungi which form a black coating on leaves in warm climates; they are purely epiphytic and saprophytic, subsisting on the "honey dew" excreted by insects, and doing little damage, as they seldom form a coating thick enough to interfere with the light supply.

In several species an extraordinary variety of accessory spores is produced. Thus *Meliola Penzigi*, the sooty mould of the orange, has conidia which differ little from vegetative cells, multicellular conidia, conidia borne in small spherical pycnidia, and conidia abstracted from conidiophores in conceptacles; perithecia are comparatively rare.

Microthyriaceae

The aerial mycelium of the Microthyriaceae is dark-coloured and superficial; the perithecia are flattened and shield-shaped, with

[1] Winge, 1911; Bezssonof, 1914.

only the upper part of the sheath fully developed. The asci are cylindrical or pyriform, and the spores are frequently bicellular. The perithecium may open by a definite ostiole, as in *Microthyrium*, or may become torn at the apex, as in *Asterina*. These two genera, with about forty and ninety species respectively, and *Asterella*, with sixty, are the largest in the family. The species are mainly tropical epiphytes on leaves, with few representatives in Europe or North America[1].

EXOASCALES

The Exoascales include the single family Exoascaceae, characterised by the type and arrangement of the asci, which are cylindrical in form, parallel in arrangement, and unprotected by a sheath; no sexual organs are known; cells of the mycelium on which the asci arise can sometimes be seen to contain two nuclei, and fusion occurs in the young ascus. It is open to question whether the parallel arrangement of the asci has any phylogenetic significance, and is not rather the result of their development near the surface of the infected carpel or leaf. A derivation of the alliance has been proposed from the Protomycetales through *Taphridium*, the ascus being regarded as equivalent to the sporangial sac, and the thick-walled segment at its base in *Taphrina aurea* and other species being homologised with the chlamydospore. There does not, however, at present appear to be sufficient evidence to support this ascription. The cylindrical form of the ascus does not suggest a primitive group, and might be held to indicate that the Exoascales are derived from one of the alliances with parallel, protected asci.

The Ascocorticiaceae, containing the saprophytic genus *Ascocorticium* with five species, are sometimes associated with the Exoascaceae; here also the asci are cylindrical, parallel, and unprotected.

EXOASCACEAE

The Exoascaceae[2] are obligate parasites upon vascular plants; they cause hypertrophy of the infected region, stimulating cells of the permanent tissue to renewed growth and division, and producing red, yellow or purple discolorations, blisters, curling of the leaf, malformation of the fruit, or the development of the bunches

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[1] Thiessen, 1913, 1914.

[2] Knowles, 1887; Juel, 1901–2, 1921; Ikeno, 1903 i; Martin, E. M., 1924, 1925.

of fasciated twigs known as witches' brooms. They are responsible for several diseases of economic importance, including peach leaf curl, induced by *Exoascus deformans*, a witch's broom on cherries caused by *E. Cerasi*, and the distortion known as pocket plums, due to the presence of *E. Pruni*, which infects the flesh of the fruit and inhibits the development of the stone.

Infection takes place when the buds of the host open, apparently
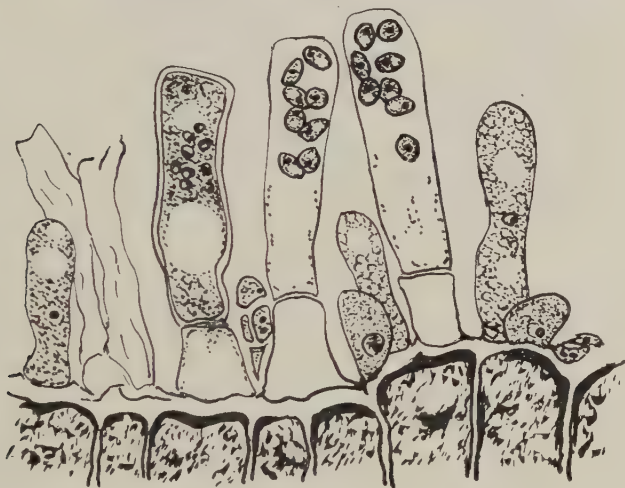
Fig. 112. *Exoascus deformans* (Berk.) Fuck., × 1000.

by means of spores deposited on the bud scales; in cold, moist weather, when the young leaves are in a state of lowered vitality, the fungus readily gains entrance; it can be checked by the use of appropriate sprays, but at a later stage destruction of the infected parts is the only treatment. Once in the leaf the hyphae, in most cases, ramify between the cells of the host, but in *Taphrinopsis Laurencia* on *Pteris biaurita* they are intracellular. Haustoria are not developed; the mycelium may be annual or perennial.

Fertile hyphae are found mainly in the leaves and carpels; sometimes the mycelium permeates the whole tissue, and asci arise below the epidermal cells, and push up among them, as in *Taphrina aurea* on the poplar; sometimes the asci originate between the epidermal cells, as in *Magnusiella Potentillae*, but in most cases, as in *Exoascus deformans*, they are developed above

the epidermal cells and just below the cuticle. In *Taphrinopsis*, on *Pteris*, the asci are formed inside the epidermal cells.

Each ascus may be borne on a short, wide stalk (fig 112)
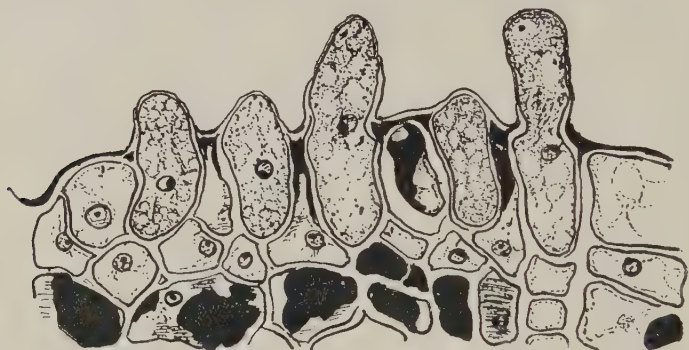
Fig. 113. *Taphrina aurea* (Pers.) Fr.; young asci, × 500.

which is cut off from the parent cell during development, or it may arise directly from the mycelium (figs. 113, 114). The divi-
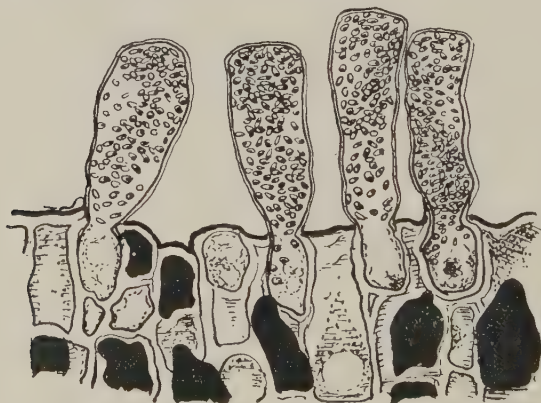
Fig. 114. *Taphrina aurea* (Pers.) Fr.; mature asci, × 500.

sions in the ascus have been shown to be karyokinetic, but the nuclei are small and details have not been elucidated.

The principal genera are *Exoascus* and *Taphrina*; in the former eight ascospores (fig. 112) are shed, in the latter (fig. 114) the spores bud while still in the ascus, giving rise to numerous, small conidia, which have caused early investigators to suggest a relationship between the Exoascaceae and the yeasts.

DISCOMYCETES

The term Discomycetes is applied to those Ascomycetes in which the fruit is open and more or less cup-shaped at maturity, and to their immediate allies. The ascocarp possesses a sheath of interwoven hyphae which is closed at first and later pushed open by the growth of the paraphyses so that it forms the outer wall of the cup. The lower part of the cup is filled by the **hypothecium**, a tangle of hyphae, some vegetative, some ascogenous. These give rise to the subhymenial layer, where the paraphyses have their origin and the young asci are developed. The asci and paraphyses together form the hymenium or fertile disc, which is spread over the surface of the interior of the cup. The asci are cylindrical and stand parallel one to another and to the paraphyses; they usually open by a lid, or by the ejection of a plug.

This characteristic, discomycetous ascocarp, or apothecium, is well seen in the Pezizales; it may be connected, through the Patellariaceae and their allies, with the fructifications of the Phacidiales, which are partly closed, developing a more or less stellate aperture, and with the elongated fructifications of the Hysteriales, which open by a narrow slit. It may be related also to the reflexed ascocarp of *Rhizina* and *Sphaerosoma*, and, by invagination of the fertile surface, with the secondarily closed fruit of the truffles. In many species the ascocarp is stalked, and from such forms the stalked Helvellales may perhaps be derived.

The sexual apparatus is known in detail only among the Pezizales. Here the antheridium is commonly a large, coenocytic structure, and never becomes detached to form a spermatium. In the simplest forms the archicarp consists of a multicellular stalk, a unicellular, coenocytic oogonium, and a short, unicellular trichogyne; this is the arrangement in *Ascodesmis*, where the oogonium becomes septate after fertilisation. A very similar oogonium is found in *Eurotium* and other Plectascales, and there is reason to regard it as the primitive female organ among Discomycetes. From it may be derived the spherical oogonium of *Pyronema*, with a unicellular trichogyne, and that of *Lachnea stercorea*, in which the trichogyne consists of four to six cells. Such spherical oogonia give rise to ascogenous hyphae without undergoing septation. In

Ascobolus furfuraceus, also, ascogenous hyphae are derived from only one cell, but in several of the Ascobolaceae and in *Lachnea cretea* they are formed from three or more cells which are in communication by means of wide pores and constitute an oogonial region; the trichogyne in such cases is always multicellular and sometimes branched, but the passage through it of male nuclei has not yet been observed. This type of archicarp, like that with the spherical oogonium, may well have been derived from such a form as *Ascodesmis*. In the Discomycetes, as in other groups of Ascomycetes, apogamy is common.

The Discomycetes include over 4000 species and may be subdivided as follows:

Hymenium fully exposed at maturity

  Mature ascophore cup-shaped   PEZIZALES

  Mature ascophore reflexed or stalked, fertile region often convoluted   HELVELLALES

Hymenium covered at maturity   TUBERALES

Hymenium incompletely exposed at maturity

  Ascophore round, aperture usually stellate   PHACIDIALES

  Ascophore elongated, opening by a slit   HYSTERIALES

PEZIZALES

The Pezizales are characterised by their fleshy or sometimes leathery ascocarp, bounded, except in the Pyronemaceae, by a more or less definite peridium which is closed at first, and is later pushed open by the growth of a conical mass of paraphyses, giving the mature fruit its cup or saucer shape.

The asci contain usually eight, but sometimes four, or sixteen, or a larger number of spores, which, in a few cases, give rise by budding to conidia. Accessory spores, including conidia of several kinds, chlamydospores, and oidia are also produced. The mycelium is well developed. Sclerotia are rare.

The following families are included in the alliance:

Peridium fleshy, continuous with hypothecium

  Peridium incomplete; ascocarps usually compound   PYRONEMACEAE

  Peridium well-developed

    Asci not rising above the surface when ripe; ascospores usually uniseriate   PEZIZACEAE

    Asci rising above the surface when ripe; ascospores often coloured and biseriate   ASCOBOLACEAE

Peridium fleshy, distinct from hypothecium
   Peridium of elongated hyphae (pseudoprosenchy-
     matous)   HELOTIACEAE
   Peridium pseudoparenchymatous   MOLLISIACEAE
  Peridium absent or ill-defined; epithecium[1] formed   CELIDIACEAE
  Peridium tough; epithecium formed
    Ascocarp free   PATELLARIACEAE
    Ascocarp embedded when young   CENANGIACEAE
  Apothecia numerous, sunk in a stroma   CYTTARIACEAE

PYRONEMACEAE

The Pyronemaceae are a small family distinguished from other
Pezizales by the slight development of the peridium. The prin-
cipal genera are *Ascodesmis* and *Pyronema*.

Ascodesmis nigricans[2] (fig. 115) is a small, coprophilous form
which grows readily in artificial culture. About forty-eight hours
after the germination of
the spore, stout, multi-
nucleate hyphae grow up
from the mycelium (fig.
116 *a*) and dichotomise to
form a group of six to
eight archicarps. Near
these, usually from the same
filament, one or two anthe-
ridial hyphae arise, grow
towards the archicarps (fig.
116 *b*) and dichotomise (fig.
116 *c*), while around each
of their terminal cells, or
antheridia, an archicarp be-
comes wrapped (fig. 116 *d*).
Walls are laid down, so
that each archicarp and

Fig. 115. *Ascodesmis nigricans* Van Tiegh.;
apothecium, × 340; after Claussen.

antheridial branch is cut off from its parent cell, and each
archicarp is divided transversely to form a trichogyne, oogo-
nium, and stalk. The trichogyne usually contains two nuclei,
the oogonium five or six, and the antheridium about the same
number. The nuclei of the trichogyne degenerate, the wall be-

[1] Cf. p. 195.   [2] Claussen, 1905.

tween this cell and the antheridium breaks down, and the male
nuclei pass into the trichogyne and thence, on the disappearance
of the intervening wall, into the oogonium. Fusion of the male
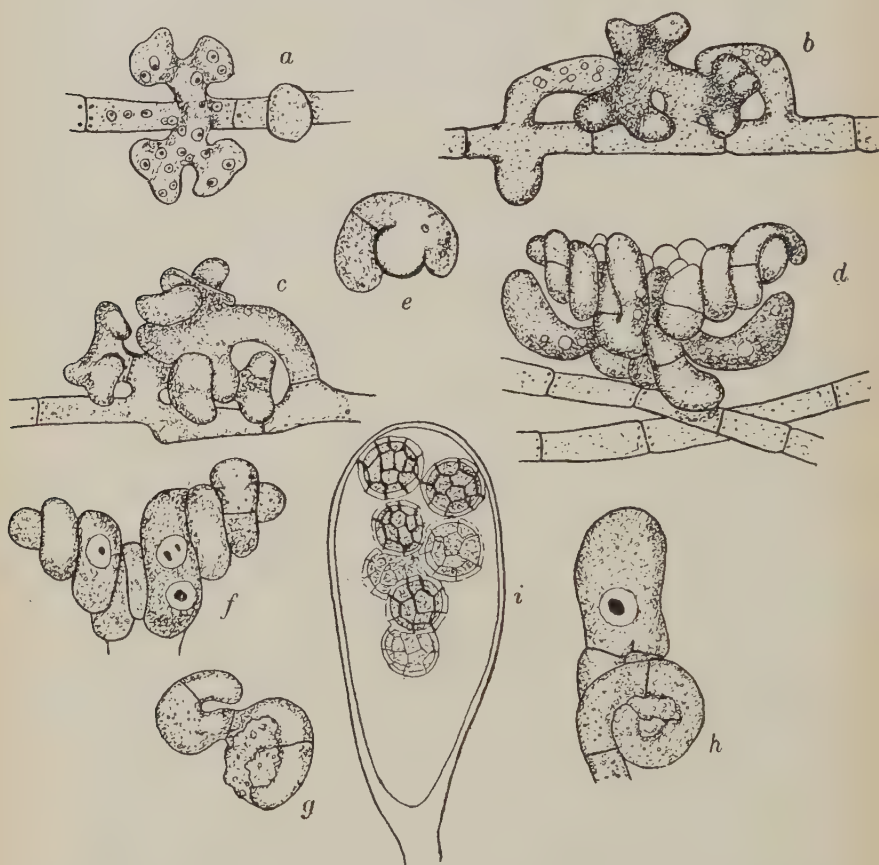
Fig. 116. *Ascodesmis nigricans* Van Tiegh.; *a, b, c, d,* development of the sexual
apparatus; *a* and *b,* × 1000, *c,* × 1100, *d,* × 800; *e,* communication between
antheridium and trichogyne, × 1300; *f,* fusion in oogonium, × 1600; *g,* septate
oogonium and ascogenous hypha; antheridium and trichogyne shrivelled,
× 1000; *h,* uninucleate ascus, × 1100; *i,* sculptured spores in ascus, × 750;
after Claussen.

and female nuclei in pairs takes place (fig. 116 *f*), the oogonium
enlarges and undergoes septation, large ascogenous hyphae, usually
three in number, are formed and quickly give rise to asci. The

ascospores are spherical (fig. 116 *i*) with a characteristically sculptured epispore.

Pyronema confluens[1] occurs on burnt ground or decaying leaves; the mycelium is superficial, the ascocarps pink or salmon coloured, and the sexual apparatus unusually large.

Filaments grow upwards from the substratum and branch dichotomously (fig. 117 *a*), much as in *Ascodesmis*; their terminal cells are differentiated as an elongated antheridium and a globose oogonium; both are multinucleate from their first formation. Very soon a slight elevation appears on the surface of the oogonium, and elongates rapidly to form the multinucleate, unicellular trichogyne, which is cut off from the oogonium by a transverse wall. The trichogyne and antheridium grow towards one another, the tip of the trichogyne meeting sometimes the apex, but more often the flank of the male organ (fig. 117 *b*). The nuclei of the trichogyne now degenerate, the walls separating the antheridium and trichogyne break down, and a thick-rimmed pore is formed through which the male nuclei stream into the trichogyne.

Fig. 117. *Pyronema confluens* Tul.; *a*, development of sexual apparatus; *b*, mature oogonia and antheridia; × 390; after de Bary.

The wall at the base of the trichogyne is next ruptured, the male nuclei travel into the oogonium and mingle with the female nuclei which are aggregated in the middle of the organ (fig. 118 *a*). When the migration of the male nuclei is complete, a fresh wall is laid down across the base of the trichogyne.

The fertilisation stage is now reached, and Harper has recorded the union of the sexual nuclei in pairs (fig. 118 *b*, *c*); according to Claussen, however, they do not fuse, but become associated (fig. 119 *b*) in preparation for their ultimate fusion in the ascus. In confirmation of this interpretation Claussen has called attention to the

[1] de Bary, 1863 ii; Tulasne, 1866; Harper, 1900; Brown, W. H., 1909, 1915; Claussen, 1912; Robinson, 1926 ii.
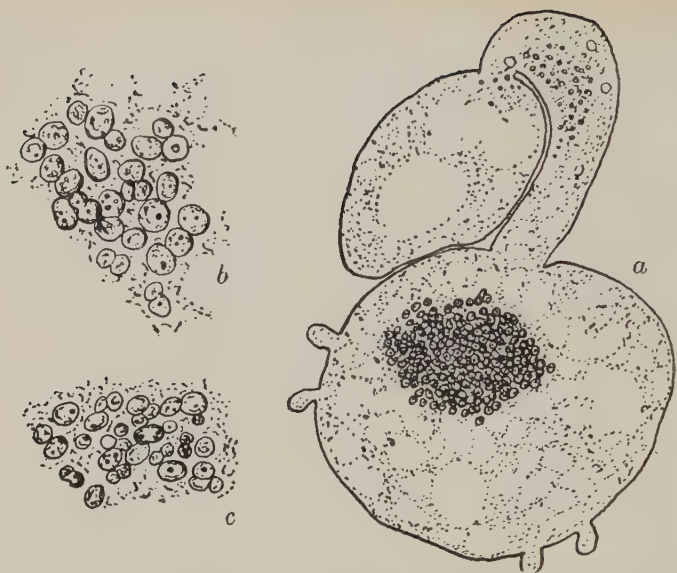
Fig. 118. *Pyronema confluens*; *a*, antheridium, trichogyne and oogonium, male and female nuclei collected in the middle of the last named; *b, c*, fusion of male and female nuclei; after Harper.
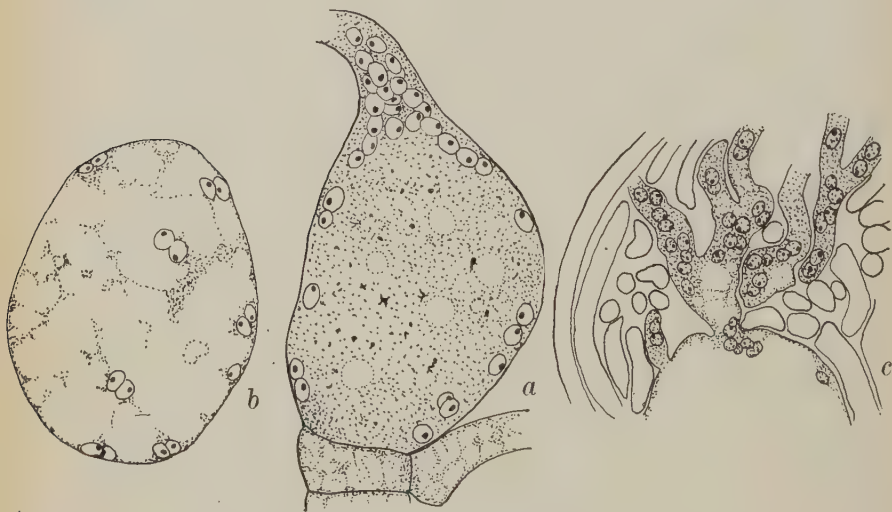
Fig. 119. *Pyronema confluens*; *a*, entrance of male nuclei into oogonium, × 1435; *b*, association of male and female nuclei, × 1160; *c*, ascogenous hyphae with nuclei in pairs, × 820; after Claussen.

occurrence of a number of paired nuclei in the ascogenous hyphae; there is, however, nothing to show that such pairs are male and female, or that they are not the product of rapid nuclear division, as in vegetative filaments. Apogamous varieties[1] of *Pyronema confluens* have also been described, in which the antheridium and trichogyne do not fuse, or the male nuclei, after entering the trichogyne, fail to reach the oogonium; in one such form[2] five chromosomes, the haploid number, have been seen throughout development. Varieties are to be expected in which the male nuclei enter the oogonium but do not pair with the female nuclei.

Fig. 120. *Pyronema confluens*; diagrammatic section through ascocarp; after Harper.

Whatever the behaviour of the sexual nuclei, the oogonium soon begins to bud out ascogenous hyphae (fig. 119 c); these ramify among the vegetative filaments, till at last their tips bend over, and asci arise from their penultimate cells, growing up among the paraphyses which the vegetative filaments have produced (fig. 120). The number of gemini in the first division in the ascus has been described as ten and as twelve.

The nuclear behaviour of this genus has been elucidated by the investigation of *Pyronema domesticum*[3], a species with pink fruits very similar to those of *P. confluens*, and often found on damp walls.

The early stages of development take place much as in *Pyronema confluens*. There is a similar archicarp with a unicellular trichogyne, and a large, globose, coenocytic oogonium from which ascogenous hyphae are budded out. The large antheridium fuses with the trichogyne, the female nuclei in the oogonium become massed together, the male nuclei enter and mingle with them, and nuclear

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[1] Dangeard, 1907; Brown, W. H., 1915. [2] Brown, W. H., 1915.
[3] Tandy, 1927.

fusions occur. The diploid number of chromosomes in *P. domesticum* is fourteen, the haploid, seven. In the ascogenous hyphae nuclear divisions are found showing fourteen chromosomes (fig. 121 *a*), the ordinary number for the sporophyte, and also divisions showing seven (fig. 121 *b*) and indicating that the divisions in

Fig. 121. *Pyronema domesticum* (Sow.) Sacc.; *a*, ascogenous hypha bending over to form ascus, nucleus in anaphase with 14 chromosomes, the diploid number; *b*, the same, nucleus in prophase, showing 7 chromosomes, the haploid number; *c*, young ascus, prophase of 1st meiotic division with 14 gemini (28 chromosomes); *d*, same, but with 7 gemini (14 chromosomes); *e*, anaphase of 1st meiotic division, with 14 chromosomes going to each pole after reduction is accomplished; *f*, anaphase of 2nd meiotic division in nuclei which are the product of only one fusion, 7 chromosomes going to each pole; *g*, telophase of 3rd division in the ascus, showing 7 chromosomes in the uncut nuclei; × 1600; after Tandy.

question are those of nuclei which did not fuse. Similarly, after the fusion in the ascus, tetraploid nuclei are found with twenty-eight chromosomes forming fourteen gemini (fig. 121 *c*), and diploid nuclei with fourteen chromosomes forming seven (fig. 121 *d*). After reduction, in the telophase of the first division, in all

stages of the second, and in the prophase of the third, there are diploid nuclei, with fourteen chromosomes (fig. 121 *e*), and haploid nuclei, with seven (fig. 121 *f*). Only, in the third telophase, all nuclei alike have seven chromosomes (fig. 121 *g*), showing that all have reached the haploid condition, and that a second reduction has taken place in those nuclei which were still diploid after meiosis. It seems clear from this evidence that *Pyronema domesticum* is in the transition state between normal sexuality combined with a second fusion in the ascus, and the complete loss of the former. The case is of special interest because male and female nuclei are actually present together in the oogonium from which the ascogenous hyphae receive unfused as well as fusion nuclei. There is some suggestion that the former occur in the first formed filaments, the female elements being stimulated to activity by the entrance of the male nuclei and passing into the ascogenous hyphae without waiting to fuse.

Pezizaceae

In the large family Pezizaceae the ascocarp is superficial, sessile or stalked, usually with a well-marked peridium of fleshy or waxy consistency, decaying soon after maturity. The spores, though septate in some small species, are usually continuous and hyaline; their arrangement is uniseriate. The ripe asci do not project above the level of the disc as they do in the Ascobolaceae. Most of the species are saprophytic, on the ground, on wood, or on dung. Classification depends on the shape of the spores, the size and consistency of the ascocarp, and the presence or absence of hairs.

In most of the species the fruit is fleshy and without hairs; they were formerly grouped together in the genus *Peziza*. The name is now retained for large species with a sessile or sub-sessile cup, regular in form and often two centimetres or more in diameter. The genus *Humaria* includes species with similar but smaller ascocarps which may be less than one centimetre across. In *Otidea* the apothecium is laterally split, or the edges are wavy and incurved; in *Geopyxis* and *Acetabularia* it is stalked. In *Lachnea* and in some other genera the fruit is beset with hairs, while in *Sepultaria* it is hairy and more or less sunk in the soil. The peridium in *Lachnea*, though much better developed than in *Pyronema*,

is never completely closed, as in *Humaria* or *Peziza*, across the top of the ascocarp.

Lachnea stercorea[1] forms beautiful, little, orange apothecia about four millimetres in diameter and furnished with brown, septate hairs. With *Humaria granulata* and *Ascobolus furfuraceus* it is among the common coprophilous Discomycetes, occurring with great regularity in the winter and spring on cow dung in many parts of Britain after the first crop of *Piloboli* has died down and the substratum has begun to dry.

Fig. 122. *Lachnea stercorea* (Pers.) Gill.; *a*, young archicarp, × 800; *b*, archicarp and antheridium, × 500; P. Highley del.

The archicarp (fig. 122 *a*) arises as a lateral branch of the my-celium and consists of three or more stalk cells, a large, oval oogonium containing two or three hundred nuclei, and a multi-cellular trichogyne. The antheridium is an elongated sac; it fuses with the distal cell of the trichogyne (fig. 122 *b*), and its contents pass into the latter but travel no farther. Nevertheless the de-velopment of the oogonium continues, its nuclei increase to over five hundred in number, and ascogenous hyphae bud out. Before passing into these the oogonial nuclei fuse in pairs, so that fertili-sation is here replaced by a union of female nuclei. The asco-genous hyphae branch and give rise to asci in each of which eight spores are produced. A second fusion occurs in the ascus and the

[1] Fraser, 1907.

resultant tetraploid nucleus undergoes three divisions, in the first of which there are four gemini, in the second four single chromosomes, while in the third two only, the haploid number, have been observed. The karyokinetic figures are small but very clear[1].
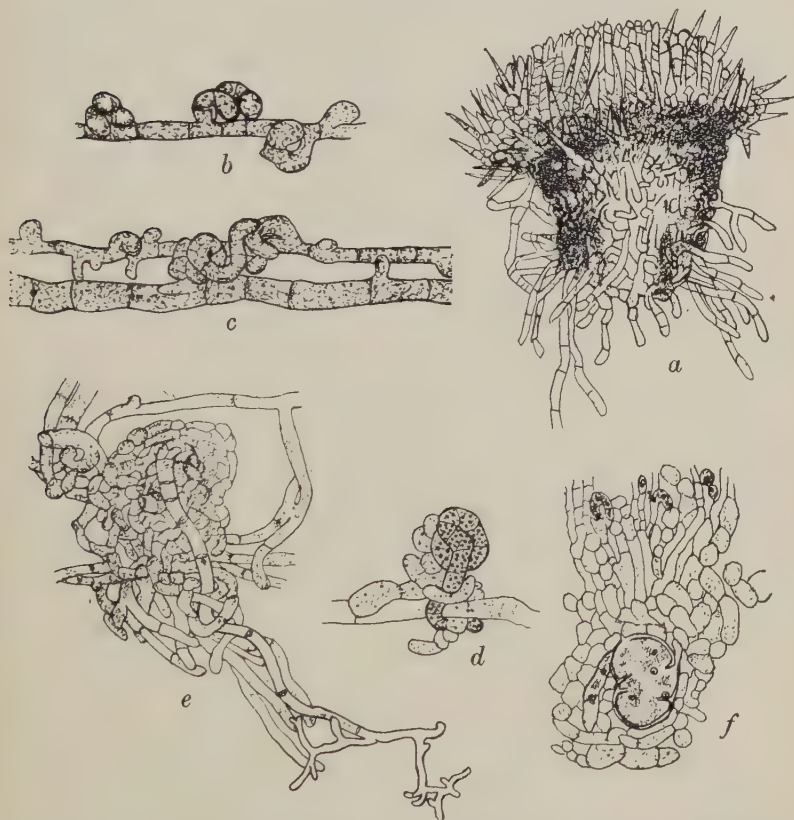
Fig. 123. *Lachnea cretea* (Cooke) Phil.; *a*, mature ascocarp, × 90; *b, c*, development of archicarp, × 300; *d*, older archicarp showing crowded nuclei, × 400; *e*, mature archicarp with elaborately branched trichogyne, × 400; *f*, oogonial region of three cells united by very large pores, × 400.

An oogonium similar to that of *L. stercorea* has been recorded for *Lachnea melaloma*[2] and also for *Lachnea scutellata*[3], which forms bright red apothecia on decaying wood.

Lachnea cretea[4] has a pale buff apothecium (fig. 123 *a*); it has

[1] Fraser and Brooks, 1909.   [2] Dodge, 1914.
[3] Brown, W. H., 1911.   [4] Fraser, 1913.

been found on plaster ceilings, and, like many other saprophytic Discomycetes, grows readily in culture. The mycelium produces numerous conidia[1] on branched conidiophores (fig. 124). The

Fig. 124. *Lachnea cretea* (Cooke) Phil.; stages in the development of the conidia, × 280; after Gwynne-Vaughan and Williamson.

archicarp has a multicellular stalk, an oogonial region of three or four coenocytic cells, and a long, branched, multicellular trichogyne (fig. 123). No antheridium has been observed. In the trichogyne pores are formed between the cells and are closed after a time by a structure resembling a callus pad. In the central part of the archicarp the transverse septa are completely broken down, so that a very wide passage is formed (fig. 123 *f*) and nuclei can pass freely from cell to cell; all the cells of this oogonial region give rise to

[1] Dodge, 1922; Gwynne-Vaughan and Williamson, 1927.

ascogenous hyphae, so that, though multicellular in origin, it is for all practical purposes unicellular at maturity and would offer

Fig. 125. *Humaria granulata* Quél.; young archicarp, × 320; after Blackman and Fraser.

no greater obstacles to fertilisation than the oogonium of *Pyronema* itself.

The branched trichogyne is exceptional among Discomycetes; it may no doubt have facilitated the establishment of contact with an attached antheridium if the latter were developed at a distance; but branching may equally be the result of a secondary, or vege-

tative activity, appearing after normal fertilisation had ceased to occur.

  Humaria granulata[1] is a common, coprophilous form with dull

Fig. 126. *Humaria granulata* Quél.; *a*, fusion of nuclei in oogonium, × 3200; *b*, oogonium giving rise to ascogenous hyphae, × 1250; after Blackman and Fraser.

red or orange apothecia. The archicarp develops as a side branch from a vegetative hypha, there is a long multicellular stalk (fig. 125), and an oval or spherical oogonium, containing numerous nuclei (fig. 126 *b*); these fuse in pairs (fig. 126 *a*) and the fusion nuclei

[1] Blackman and Fraser, 1906 ii; Fraser and Brooks, 1909.

pass into the ascogenous hyphae. The haploid chromosome number is four, eight gemini are found in the tetraploid nucleus of the ascus. There is no sign of either antheridium or trichogyne.

In *Humaria rutilans*[1], a species with clear orange apothecia occurring on soil or among moss, reduction has gone still further, and not even an archicarp is produced. The apothecium arises as a weft of branching filaments which for a time differ one from another only in the relatively thick walls of the outer hyphae, and the rich protoplasmic contents of the inner (fig. 127). Each cell of the weft contains one or a few nuclei. After a while the nuclei of the central region may be seen to be of two sizes, the smaller (fig. 128 *a*) fusing in pairs to give rise to the larger; sometimes, in connection with this process, a nucleus migrates through the cell wall (fig. 128 *b*), as in the prothalli of apogamous ferns. Thus in *H. rutilans*, where sexual

Fig. 127. *Humaria rutilans* (Fr.) Sacc.; very young ascocarp, × 500.

organs are completely lacking, normal fertilisation is replaced by the union of vegetative nuclei in pairs; the cells which contain fusion nuclei give rise to ascogenous hyphae, while, from the rest, the paraphyses and cells of the peridium arise.

The number of chromosomes in the nuclei of the ascogenous hyphae is sixteen (fig. 129 *a*); there are sixteen gemini (thirty-two chromosomes) in the first division in the ascus (fig. 129 *c*), and sixteen chromosomes in the second division (fig. 130 *a*) and in the prophase of the third (fig. 130 *b*). In the third telophase there are eight chromosomes (fig. 131), indicating that a second reduction

[1] Guilliermond, 1905 i, 1913; Fraser, 1908.

Fig. 128. *Humaria rutilans* (Fr.) Sacc.; *a*, fusion in a vegetative hypha; *b*, migration of nucleus from one vegetative cell to another; both × 1100.

Fig. 129. *Humaria rutilans* (Fr.) Sacc.; *a*, ascogenous hypha showing sixteen chromosomes in each nucleus, × 1950; *b*, fusion nucleus of ascus with double spireme, × 1300; *c*, fusion nucleus of ascus showing sixteen gemini, × 1950.
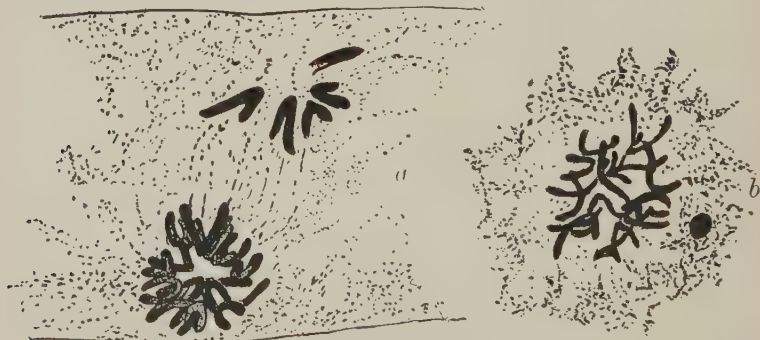
Fig. 130. *Humaria rutilans* (Fr.) Sacc.; *a*, telophase of second division in ascus, × 3370; *b*, prophase of third division in ascus, showing sixteen curved chromosomes, × 2808.

has occurred. Sixteen chromosomes have also been recorded (fig. 132) in the third telophase; if this observation is confirmed it may indicate that, as in so many angiosperms, there exists in this species an apogamous variety with double the haploid number of chromosomes.

In several other members of the Pezizaceae, such as *Peziza tectoria, Peziza vesiculosa*[1] and *Pustularia bolarioides*[2], development

Fig. 132. *Humaria rutilans*; telophase of third division in ascus; after Guilliermond.
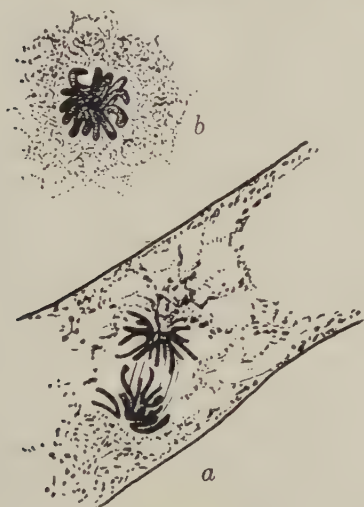
Fig. 131. *Humaria rutilans* (Fr.) Sacc.; *a*, metaphase of third division in ascus with v-shaped chromosomes, × 2080; *b*, polar view of telophase of third division, showing eight curved chromosomes, × 3100.

takes place without the formation of sexual organs. *Peziza vesiculosa*, like *Humaria rutilans*, shows evidence of pseudapogamous fusions, but *Pustularia bolarioides* appears to be euapogamous, since there are sixteen gemini in the first division in the ascus, and the same number of chromosomes in the third telophase.

In *Otidea aurantia*[1] a large cell, no doubt part of an archicarp, has been recorded in the early stages of development, and in *Peziza theleboloides, Humaria Roumegueri* and *Humaria carbonigena* there is a well-marked oogonial region of one or more cells.

[1] Fraser and Welsford, 1908.   [2] Bagchee, 1925.

Ascobolaceae

The ascocarp of the Ascobolaceae is soft and fleshy or somewhat gelatinous, and possesses a well-marked peridium by which the fruit is closed at first. The family is distinguished from the Pezizaceae by the usually multiseriate arrangement of the spores and by the fact that the ripe asci stand well above the level of the hymenium before their spores are discharged. Often the asci are large and few in number; they have a peculiar, two-lipped method of dehiscence in *Ascozonus* (fig. 133), but in other genera they open by a lid. The spores are brown or violet in *Ascobolus*, *Saccobolus* and *Boudiera*, hyaline in most of the other genera; they are usually ellipsoid, but round in *Boudiera* and *Cubonia*;

Fig. 133. *Ascozonus* sp.; ascus during and just after dehiscence, ×335; W. M. Page del.

in *Saccobolus* they are enclosed within a special membrane and ejected together; in *Thecotheus*, *Rhyparobius*, *Ascozonus* and *Thelebolus* they are sixteen or more in number.

In most of the investigated species there is a multicellular, coiled archicarp, the central cell or cells of which give rise to ascogenous hyphae. To this organ the term **scolecite** was formerly applied. Several species produce conidia or chlamydospores.

In *Ascobolus magnificus*[1], alone among Ascobolaceae, a large antheridium, similar to that of *Pyronema* or *Lachnea*, has been observed, and in this species, almost alone among Ascomycetes, the mycelium is apparently dioecious. The male and female organs originate where mycelia of different strains are brought into contact; they develop in pairs (fig. 134), the archicarp elongates, divides into a number of cells, coils round the antheridium, and fuses with it. Meanwhile the oogonium, usually the seventh or eighth cell from the fused tip, has begun to enlarge, and ascogenous hyphae soon grow out, originating from only one cell. Nuclear details are not yet available.

Ascobolus carbonarius[2] occurs on burnt ground among charcoal. The ascocarp is scurfy and green or brown in colour. Numerous conidia are formed on the mycelium, and it is from one of these,

<hr>

[1] Dodge, 1920.　　　　[2] Dodge, 1912.

germinating while still attached to its stalk, that the archicarp is stated to arise. It has a multicellular stalk, a fertile region of some
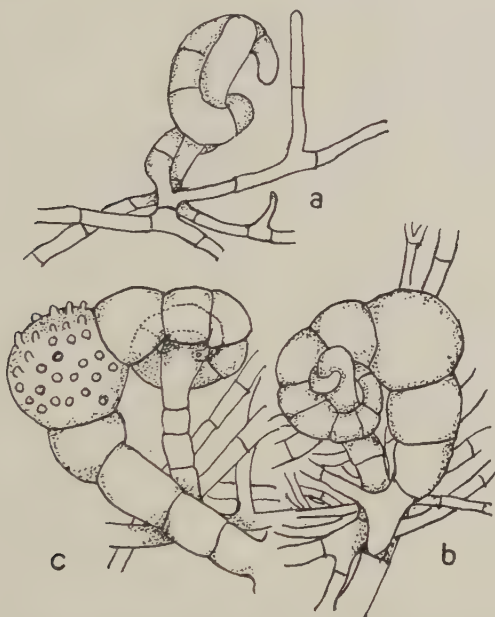
Fig. 134. *Ascobolus magnificus* Dodge; *a*, archicarp wound spirally round antheridium; *b*, older antheridium and archicarp, showing usual arrangement; *c*, ascogenous hyphae budding out from oogonial cell; after Dodge.

Fig. 135. *Ascobolus carbonarius* Karst.; archicarp, × 280; after Dodge.

twenty to forty cells from which the ascogenous hyphae arise, and a terminal trichogyne of ten to twenty cells. The apex of the trichogyne (fig. 135) is found to wrap itself round a second coni-

dium, attached, like the first, to its stalk. It is possible that this conidium functions as an antheridium, but cytological details are not known.

Ascobolus furfuraceus[1] is one of the common coprophilous species; here, also, the ascocarp is green or brown, with a characteristically scurfy margin. The archicarp (fig. 136) may consist of seven to as many as twenty cells, each of which, when mature, contains several nuclei. One near the middle of the row enlarges to form the oogonium and is brought into communication with its neighbours by means of pores (fig. 137 *b*). Additional nuclei pass into it from the cells of the trichogyne and stalk, nuclear fusions take place, the fused nuclei

Fig. 136. *Ascobolus furfuraceus* Pers.; archicarp, × 740; after Dodge.

enter the ascogenous hyphae and reach the ascus in the usual way.
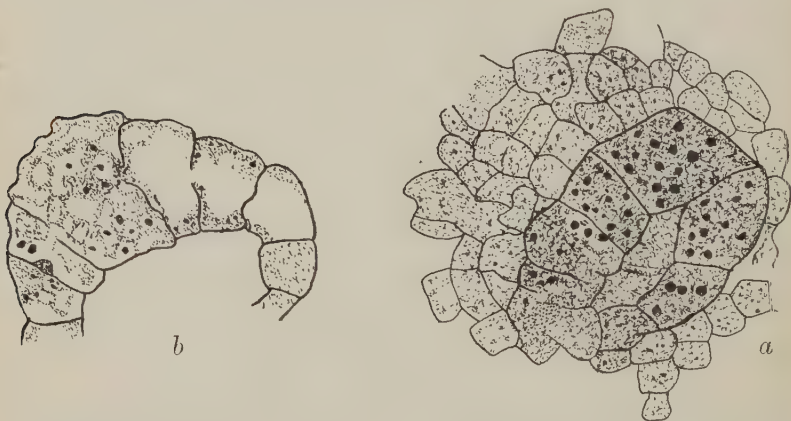
Fig. 137. *Ascobolus furfuraceus* Pers.; *a*, young archicarp, × 750; *b*, rather older specimen showing pores between the cells, × 625; after Welsford.

There are eight chromosomes in the first division in the ascus and four[2] in the second and third.

In *Ascobolus citrinus*[3] and *Ascobolus immersus*[4], as in *Ascobolus furfuraceus*, only one cell gives rise to ascogenous hyphae; in the former species the pores between the oogonial cell and its neigh-

[1] Harper, 1896; Dángeard, 1907; Welsford, 1907.
[2] Dangeard, 1907; Fraser and Brooks, 1909.   [3] Schweizer, 1923.
[4] Ramlow, 1914.

bours are particularly well marked and extend to the distal end of the trichogyne. In both species the only fusion seen was that in the ascus. In the archicarp of *Ascobolus glaber*[1] there are twenty to thirty cells, from one or more of which ascogenous hyphae are developed, while in *Ascobolus Winteri*[1] (fig. 138), a form occurring on goose dung and apparently limited to that habitat, ascogenous hyphae arise from several cells.

The genus *Ascophanus* differs from *Ascobolus* chiefly in the
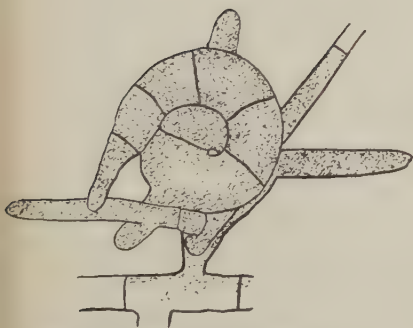
Fig. 138. *Ascobolus Winteri* Rehm.; archicarp, × 1080; after Dodge.

Fig. 139. *Ascophanus carneus* Pers.; old archicarp, showing associated nuclei, × 800; after Ramlow.

smooth, colourless spores. *Ascophanus carneus*[2] has red, pink or orange apothecia, occurring on the dung of cows and rabbits, on old leather, rope, and similar habitats. The archicarp is a coiled, multicellular filament, varying considerably in size and in the number of its cells. There is an oogonial region (fig. 139) of three to seven cells from all of which ascogenous hyphae arise. In the cells of the oogonial region nuclear fusions take place (fig. 140), but some observers have regarded these as pathological, assuming that the nuclei which become associated in the oogonium do not fuse but travel up the ascogenous hyphae in pairs.

The species of *Rhyparobius* and *Thelebolus*, the genera with

[1] Dodge, 1912.　　　[2] Cutting, 1909; Ramlow, 1914.

many spored asci, are minute, coprophilous forms. They are distinguished by the fact that the apothecium of *Rhyparobius* pro-
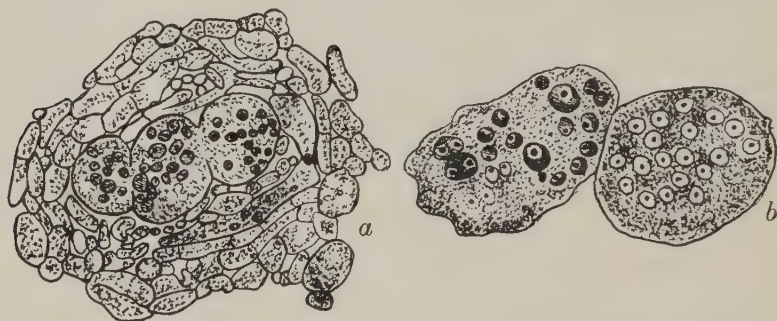
Fig. 140. *Ascophanus carneus* Pers.; *a*, section through young ascocarp, showing nuclear fusion in two cells of the archicarp, × 580; *b*, two cells of an archicarp, showing nuclear fusions, × 1240; after Cutting.

duces several large asci, and that of *Thelebolus* only one (fig. 141). In both genera the cells of the mycelium are uninucleate.

In most species of *Rhyparobius*[1] there is a single, twisted, multicellular archicarp to each fruit, but in the apothecium of *Rhyparobius Pelletieri* several have been described. In this species eight free nuclei are formed as usual in the ascus; they go through a period of rest and growth and then divide further till thirty-two are present; around these the spores are delimited.

In *Thelebolus stercoreus*[2] the primordium of the ascocarp is a thick branch containing a single nucleus. Later, two, four, and finally eight nuclei are seen (fig. 142) and septation takes place so

Fig. 141. *Thelebolus stercoreus* Tde.; ascocarp with single ascus, × 250; after Brefeld.

that a row of cells is formed. One of these contains two nuclei; it enlarges and becomes the single ascus; the two nuclei fuse (fig. 143). The definitive nucleus divides karyokinetically, some-

[1] Barker, 1903, 1904; Overton, 1906.　　[2] Brefeld, 1891; Ramlow, 1906.

times as many as ten times, so that 1024 nuclei are formed. The morphology of the septate branch in this fungus is difficult to interpret; since one of its cells becomes an ascus it does not at

Fig. 142. *Thelebolus stercoreus* Tde.; development of archicarp, × 1750; after Ramlow.

first sight seem comparable with the archicarp of *Ascobolus*. The condition, however, in the Erysiphaceae may be borne in mind, where the penultimate cell of the archicarp, after fertilisation, gives rise in *Erysiphe* to ascogenous filaments, while in *Sphaerotheca* it

Fig. 143. *Thelebolus stercoreus* Tde.; *a*, young ascocarp with binucleate asci; *b*, ascus containing fusion nucleus, both × 810; after Ramlow.

becomes itself the single ascus. It would not be impossible to compare *Sphaerotheca* and *Thelebolus* and to regard them as showing corresponding stages of reduction. In the Erysiphaceae, however, the formation of the ascus, alike in *Erysiphe* and *Sphaerotheca*, is preceded by normal fertilisation.

HELOTIACEAE AND MOLLISIACEAE

The members of these families are distinguished from the Pezizaceae by the fact that their peridium differs in structure from the hypothecium. In Helotiaceae the peridium is prosen-

chymatous, composed of elongated, parallel hyphae, usually light in colour and thin walled. In Mollisiaceae it is parenchymatous, of round or polygonal cells, usually thick and dark coloured. In both families the ascus opens by the ejection of a plug, and not, as in most Discomycetes, by a lid.

The apothecia in both families are small, often stalked, sometimes growing out from a sclerotium; they are waxy in consistency and may be glabrous or hairy. Most species are saprophytes, often occurring on dead plants. In Helotiaceae the apothecium is sunk in the substratum, in Mollisiaceae it is frequently superficial.

Among the Mollisiaceae *Pseudopeziza Trifolii* is parasitic and causes the leaf spot disease of clover. The leaves become spotted and finally die, so that the crop is injured. There are many other species of *Pseudopeziza*, several on dead stems and leaves, a few on the living tissues of wild plants.

Another parasite of some importance is *Dasyscypha Willkommii*[1], the well-known larch canker. The apothecia are externally yellow with an orange disc; the ascospores give rise to germ tubes which cannot penetrate the bark, but obtain entrance through wounds caused by hail, ice or snow, or by the attacks of insects. The mycelium ramifies chiefly in the soft bast, but may penetrate the wood as far as the pith. Where it spreads into the bark the tissues shrivel, producing depressed canker spots in which the white stromata develop. These give rise to minute, unicellular conidia, and, later, if conditions are moist, to ascocarps.

In the genus *Sclerotinia* the stalked ascocarps arise from sclerotia (fig. 144). Many of the species are parasitic; *S. tuberosa* on *Anemone nodosa*, *S. trifoliorum*[2], the fungus of clover rot, on clover, *S. sclerotiorum* on the potato, cabbage and other hosts, *S. fructigena* and *S. cinerea* on species of *Prunus* and *Pyrus* where they give rise to brown rot, blossom wilt and other pathological conditions. In the case of *S. cinerea*[3], the cause of brown rot on plums, the shoots of the infected tree are killed soon after their leaves unfold, and the mycelium extends from the dead shoots into the twigs that bear them, producing cankers above and below which the xylem elements are destroyed. Conidia occur on the leaves and may infect

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[1] Hiley, 1919.　　　　[2] Wadham, 1925.
[3] Wormald, 1919, 1920, 1922.

new trees; the ascigerous stage is found on mummified plums. In *S. sclerotiorum* and *S. trifoliorum* sclerotia appear in the stems; in the latter species the apothecia which develop from them expand only in the presence of light. Conidia are produced in bunches such as characterise the form genus *Botrytis*, or in chains as in the form genus *Monilia*[1].

CELIDIACEAE, PATELLARIACEAE AND CENANGIACEAE

In the families already described the ascocarp is either fleshy or waxy, in Celidiaceae, Patellariaceae and Cenangiaceae it is
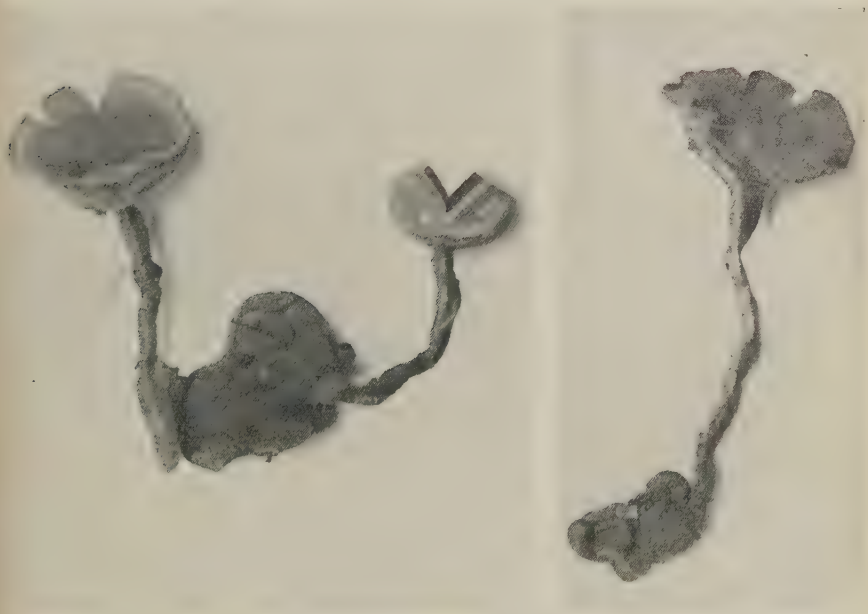
Fig. 144. *Sclerotinia tuberosa* (Hedw.) Fuck.; sclerotia and apothecia, nat. size.

leathery, horny, or cartilaginous, and the ends of the paraphyses are interwoven above the asci to form a layer known as the **epithecium**. The ascospores are sometimes more than eight in each ascus, and may be one to many-celled; in some species pycnidia

[1] Cf. p. 317.

are present. The three families are sometimes grouped together as Dermateaceae.

Bulgaria polymorpha[1], one of the best known of the Cenangiaceae, occurs on dead trunks of trees, especially beech. The ascocarps burst through the bark as small, rusty brown, scurfy knobs, which gradually expand, exposing the black and shiny hymenium; the substance is soft and tough, resembling india-rubber in consistency and appearance. The species is readily distinguished by its four, slightly curved, brown ascospores associated with four abortive spores.

The genus *Coryne* is possibly related to *Bulgaria*. *C. sarcoides* is a common species on rotten trunks and stumps. The apothecia are crowded together and are dull red or purple in colour. The conidial fructifications occur among them or alone; their stromata are rather paler in colour than the apothecia and bear fertile hyphae from the ends of which minute conidia are abstricted.

CYTTARIACEAE

This very curious family[2] contains the single genus *Cyttaria* (fig. 145). Six species are known, occurring in New Zealand, Tasmania and South America; all are parasitic on species of *Nothofagus*.

C. Darwinii was collected in Tierra del Fuego by Darwin in 1833. "In the beech forests," he says, "the trees are much diseased; on the rough excrescences grow vast numbers of yellow balls. They are of the colour of the yolk of an egg, and vary in size from that of a bullet to that of a small apple; in shape they are globular, but a little produced towards the point of attachment. They grow both on the branches and stems in groups. When young they contain much fluid and are quite tasteless, but in their older and altered state they form a very essential article of food for the Fuegian." He observed that the whole surface is "honeycombed by regular cells." These are the separate apothecia, considerable numbers of which occur on the same stroma. Unfortunately the details of development are still unknown.

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[1] Biffen, 1901.
[2] Berkeley, 1842, 1847 ii, 1848; Fischer, 1886; Buchanan, 1895.

Fig. 145. *Cyttaria Gunnii* Berk.; *a*, twig of *Nothofagus Cunninghami* with knobs bearing the fungus, × $\frac{2}{5}$; *b*, group of stromata; *c*, single stroma cut across; all after Berkeley.

HELVELLALES

The members of this alliance are saprophytes, growing chiefly on the ground, in some cases on decayed wood. Most have large, fleshy and stipitate ascophores with the hymenium spread over the upper surface and covered at first by a veil or membrane. Such a fructification may perhaps be homologised with a stalked *Peziza*,

in which the cup is turned inside out during the early stages of development; the structure is often complicated by extensive convolutions of the fertile surface.

There are three families:

Ascophore flattened, not stalked   RHIZINACEAE

Ascophore stalked

    Fertile region of head distinct from stalk, ascus
      opening by a lid   HELVELLACEAE
    Fertile region not always distinct from stalk, ascus
      opening by a plug   GEOGLOSSACEAE

RHIZINACEAE

The Rhizinaceae include two genera, *Rhizina* and *Sphaerosoma*. *Rhizina* has a flattened, crust-like, superficial ascocarp, more or less concave below and attached to the soil by strands of mycelium, while in *Sphaerosoma* the ascocarp is partly sunk in the substratum and the rooting hyphae are sometimes grouped on a short pedicel. It is concave when young (fig. 147), but later becomes strongly reflexed (fig. 146).

Fig. 146. *Sphaerosoma fuscescens* (Klotz.) Roup.; apothecium, $\times 6$; after Rouppert.

Rhizina inflata is known to occur in Great Britain only as a saprophyte growing on soil, but, both in France and Germany, it has been found to attack conifers. The mycelium ramifies in the intercellular spaces and forms masses of pseudoparenchyma in dead and diseased tissues of the host. The trees lose their needles and die.

In *R. undulata*[1] the development of the apothecium is preceded by the appearance of a long, multicellular archicarp recalling that of the Ascobolaceae.

In *Sphaerosoma Janczewskianum*[2] a large oogonial cell has been described from which the ascogenous hyphae originate.

[1] Fitzpatrick, 1918.   [2] Rouppert, 1909.

HELVELLACEAE

The Helvellaceae include six genera, *Helvella* (fig. 148 *a*), *Morchella* (fig. 148 *b*, *c*), *Verpa*, *Gyromitra*, *Cidaris* and *Cudoniopsis*[1]; of these the first four are British. In all a definite fertile head is distinguished from the stalk, and over the more or less convoluted
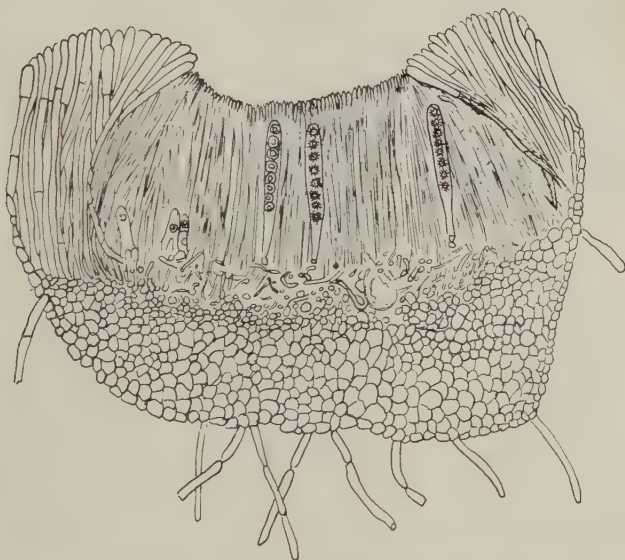
Fig. 147. *Sphaerosoma Janczewskianum* Roup.; apothecium showing asci and paraphyses, × 70; after Rouppert.

surface of the head the hymenium extends. Development has been studied only in *Helvella*[2], where the fruit arises as a tuft of branching, septate hyphae, the outer of which form a protective membrane, broken as growth proceeds to expose a palisade of club-shaped filaments. An oogonium has not been observed.

In *Helvella crispa*[3] apogamous fusions, similar to those in *Humaria rutilans*, have been recorded in the vegetative cells of the hymenium, and both in this species and in *Morchella esculenta*[4] the third division in the ascus appears to bring about a second reduction in the number of chromosomes.

[1] Spegazzini, 1925.   [2] McCubbin, 1910.
[3] Carruthers, 1911.   [4] Maire, 1905.

GEOGLOSSACEAE

The Geoglossaceae grow usually in damp or moist situations such as low, wet woods or shady slopes. They occur on soil, or on dead branches or leaves, and two species of *Mitrula* are parasitic on moss. There are eight genera, five of which are British.

The ascophore is erect and stipitate, the terminal, fertile region

Fig. 148. *a*, *Helvella crispa* (Scop.) Fr.; *b* and *c*, *Morchella vulgaris* Pers.; after Boudier.

being club-shaped (fig. 149 *a*), laterally compressed, or forming a cup, or a pileus (fig. 149 *c*). In some of the simpler forms, as in *Geoglossum hirsutum*, there is no clear line of demarcation between the fertile and sterile regions. The ascus contains eight spores and opens by the ejection of a plug.

The young ascocarp consists, as in *Helvella*, of a tangle of vegetative hyphae and is commonly protected, as in that genus, by an outer membrane or veil. In *Leotia lubrica*[1] a large,

[1] Massee, 1897; Durand, 1908; Brown, W. H., 1910; Duff, 1922.

branching cell, presumably an oogonium, occurs at the base of the young ascocarp and appears to give rise to the ascogenous hyphae.

In the species of *Spathularia* and *Vibrissea*, as in *Geoglossum*, the spores are very long, narrow and septate, lying side by side in the ascus. *Geoglossum* is distinguished by its coloured spores (fig. 150 *a*), the other two genera, in which the spores are hyaline (fig. 150 *b*), by the form of the fructification. In the rest of the

Fig. 149. *a, Geoglossum hirsutum* Pers., nat. size; *b, Spathularia clavata* Sacc., nat. size; *c, Leotia lubrica* Pers., form *stipitata*, × ⅔; after Massee.

Geoglossaceae, as in the Helvellaceae, the spores are elliptical and hyaline, and are arranged one above the other in the ascus. They may be continuous or septate.

A relationship to the Pezizales seems not improbable, perhaps through *Leotia*, where the fertile region is pileate, to the Helotiaceae or Mollisiaceae, which resemble the Geoglossaceae in the means of dehiscence of the ascus.

TUBERALES

The Tuberales are characteristically subterranean, though some species are imperfectly buried and others grow among decaying leaves. When mature the fruits emit a powerful odour by which rodents are apprised of their whereabouts. The ascocarp is eaten

and the spores dispersed after passing through the alimentary canal of the animal.

The ascocarp is more or less globose, sometimes completely closed, sometimes with a small opening. The hymenium may form a smooth lining to the fruit, or may be thrown into elaborate folds, so that the fertile region is divided into chambers. The asci contain one to eight spores; the epispore is often elaborately ornamented at maturity.

Early investigators classed the Tuberaceae with the hypogeal Gasteromycetales; a consequence of this survives in the use of the term **gleba** to describe the contents of the fructification, including both the vegetative hyphae and the fertile cells.

The Tuberales include a single family, the Tuberaceae; their relationship is probably to the Pezizaceae and Rhizinaceae. One or

Fig. 150. *a*, *Geoglossum hirsutum* Pers., × 230; *b*, *Spathularia clavata* Sacc., × 400; after Massee.

more series can be traced from these families to the Tuberales, the principal modifications being in the direction of adaptation to subterranean conditions by the increased protection of the hymenium. This appears to have been achieved either by retaining at maturity the closed form of the young pezizaceous ascocarp, as in *Genea* and *Pachyphloeus*, or by the invagination of a prematurely exposed fertile layer, as in *Tuber*, and its protection by a secondary sheath.

TUBERACEAE

The Tuberaceae[1] include eight genera; in *Genea* the ascocarp is of the pezizaceous type, but with a somewhat convoluted hymenium (fig. 151 *b*, *c*); the asci are cylindrical and the spores

[1] Boulanger, 1904, 1906 i, ii; Bucholtz, 1908, 1910; Massee, 1909.

uniseriate. In *Stephensia* and *Pachyphloeus* the convolutions of the hymenium are more marked; the asci of *Pachyphloeus* are stouter and the spores irregularly biseriate.

In *Balsamia* the asci are broadly oblong or subglobose (fig. 152); the convolutions of the hymenium give the appearance in section of separate chambers (fig. 153); the mature ascocarp is enclosed
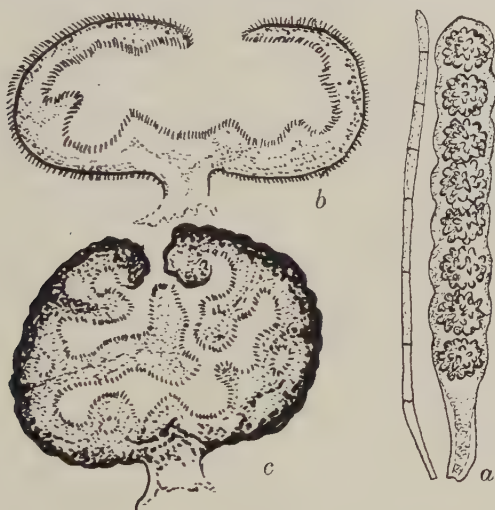
Fig. 151. *Genea Klotzchii* B. and Br.; *a*, ascus and paraphysis; *Genea hispidula* Vitt.; *b*, apothecium; *Genea sphaerica* Vitt.; *c*, apothecium; after Massee.

by a special sheath. During development the hymenial chambers communicate at several points with the exterior, indicating that they are formed by the invagination of a reflexed fertile disc similar to that of *Rhizina*.

In *Tuber* this type of structure is clearly marked. The ascocarp is irregularly globose, fleshy or in some cases almost woody; internally the walls which divide the gleba are extensively branched, and the free space between them is diminished, so that opposite layers of the hymenium are brought close together and constitute the so-called fertile "veins." Other "veins," white and sterile, run between the hymenial layers (fig. 154). The asci are often globose (fig. 155); the spores are usually four in number but are sometimes reduced to two or one.

Development is known in *Tuber puberulum*[1] (fig. 156), where

[1] Bucholtz, 1903.

the very young apothecium consists of a mass of hyphae, the outer rather more loosely interwoven than the inner. Around the lower part a dense basal sheath is differentiated, corresponding to the peridium of a cup-shaped ascocarp. Soon the first signs of the fertile veins appear as invaginations of the upper surface, which, though as yet showing no trace of asci, corresponds to the fertile disc. Owing to the rapid growth of the upper portion of the fruit, the basal sheath is bent backwards, while along the fertile veins the young asci begin to appear. Later the peripheral tissues become thickened, and, together with the basal peridium, form the special sheath.

Fig. 152. *Balsamia vulgaris* Vitt.; section through hymenium; after Tulasne.

This ultimately closes over the points where the fertile veins are in communication with the exterior.

The ascocarps of many species of *Tuber* are edible, and are

Fig. 153. *Balsamia vulgaris* Vitt.; after Tulasne.
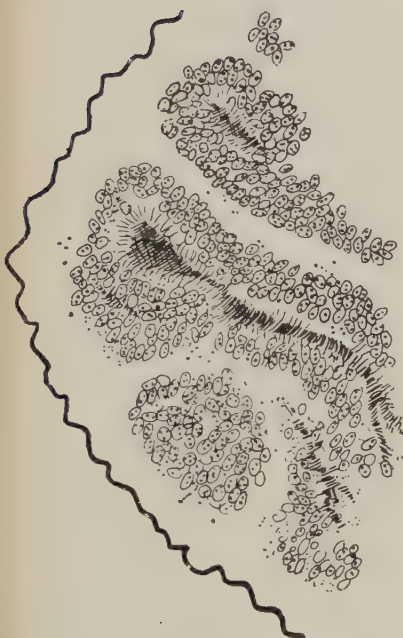
Fig. 154. *Tuber rufum* Pico; general view of fertile region; after Tulasne.

Fig. 155. *Tuber rufum* Pico; section through hymenium; after Tulasne.
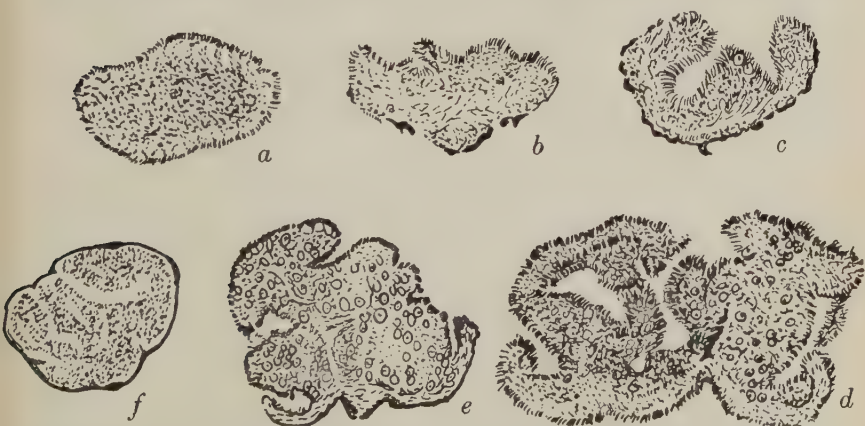
Fig. 156. *Tuber puberulum* (B. and Br.) Ed. Fisch.; *a–e*, development of ascocarp; *a*, × 52; *b* and *c*, × 28; *d* and *e*, × 21; *f*, section through mature ascocarp, × 6; all after Bucholtz.

known as truffles, the most esteemed being *T. melanosporum* which does not occur in Britain. They grow chiefly in soils mixed with clay and containing iron, or in mixed alluvium; the soil must be porous to ensure sufficient aeration. Truffles occur in chestnut, oak, and especially beech woods, and form mycorrhiza with the roots of these trees.

PHACIDIALES

In the Phacidiales the ascocarp is immersed in the substratum. It is usually small in size and leathery, waxy, or corky in consistency; an epithecium is often developed; members of this alliance differ from the Hysteriales principally in the greater exposure of their hymenium at maturity, but the cup never opens as widely as in the alliances previously considered.

There are two chief families.

STICTACEAE

The Stictaceae form a considerable assemblage of species with small ascocarps, occurring saprophytically on wood or other plant remains. Their development and minute anatomy, apart from systematic characters, are almost unknown. They have a fleshy or waxy disc, pale or clear-coloured, usually white, yellow, or tinged with pink. The peridium is not always developed: when present it is thin and white, and is mealy owing to the occurrence of particles of calcium oxalate; when the fruit opens it forms a white border around the hymenium. The pale colour of the fruit and ragged or toothed dehiscence of the sheath are characteristic.

PHACIDIACEAE

These fungi are distinguished by their black, thick-walled apothecia, usually scattered, sometimes, as in *Rhytisma*, grouped on a black stroma. Where the hymenium is circular the sheath splits in a stellate manner, but where it is elongated dehiscence takes place by means of a slit. The species occur mainly on dead herbaceous stems or leaves, but a few are parasitic.

Rhytisma Acerinum[1] (fig. 157) infects the leaves of species of *Acer*. The mycelium ramifies in the tissues of the host and causes

---

[1] Bracher, 1924; Jones, 1925.

yellow spots about three weeks after infection. Some five weeks later pycnidia develop under the cuticle in these areas and produce small, unicellular conidia. The epidermis and underlying tissues of the host become filled with hyphae and a dense, black sclerotium is completed. In this state the leaf falls off and next spring the sclerotia thicken, become wrinkled, and finally burst by elongated fissures to expose the discs of the apothecia. The ascospores are filiform and aseptate, they are ejected with some force and are
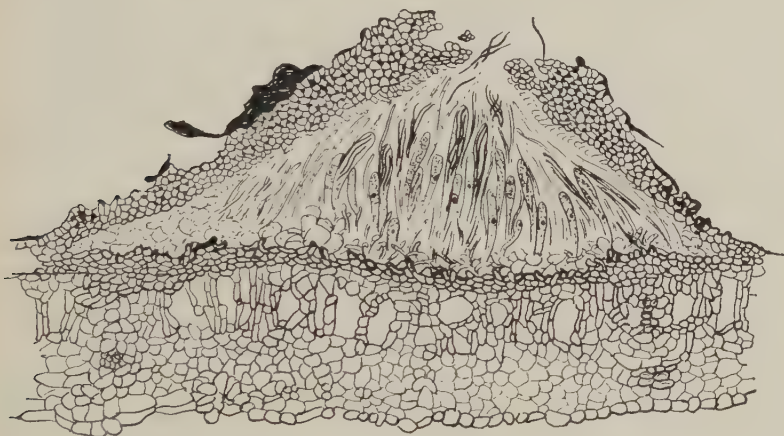
Fig. 157. *Rhytisma Acerinum* (Pers.) Fr.; apothecium, × 160.

probably conveyed to the young leaves by the wind; their germ tubes enter through the stomata.

Both in this species and in *Cryptomyces Pteridis*[1] swollen cells have been described in the sub-hymenium, but in view of their unusual position further evidence is required before their sexual significance can be accepted.

HYSTERIALES

The Hysteriales are characterised by a black, elongated asco-carp, which opens by a longitudinal slit so narrow that the greater part of the disc remains concealed.

The species are minute; in some the disc is narrowly elliptical,

[1] Killian, 1918.

in some it is stellate, in others the ascocarp is raised and laterally compressed so as to resemble a miniature mussel or oyster standing on its hinge. When the ascocarp is superficial it is rigid and carbonaceous in consistency, when developed beneath the substratum the wall is membranous. In a few cases pycnidia are known, producing oblong, unicellular, hyaline conidia.

Most of the species are saprophytic on old wood, bark, or dry leaves. The mycelium is sometimes found in the tissues of living plants, though apothecia reach maturity only after the host is dead. *Lophodermium pinastri*, for example, produces pine blight or needle cast in the seedlings of *Pinus sylvestris* and other conifers, causing them to drop their leaves. Pycnidia are first formed and ascocarps later, on the fallen needles. Mature trees are attacked and, though not themselves seriously injured, act as centres of infection in the neighbourhood of seed-beds and nurseries.

The subdivision of the Hysteriales depends on the consistency of the sheath, the form of the ascocarp, and its superficial or immersed position. Hysteriaceae and Hypodermataceae are the principal families.

In the form of their fructification the members of the Hysteriales are intermediate between the Discomycetes and Pyrenomycetes. Species differ from certain of the Phacidiales chiefly in the narrow opening of the ascocarp, and from the simpler Sphaeriales in the fact that this opening is elongated instead of round. Such ascocarps might be said to resemble not a cup or a flask but a laterally compressed jug. Further research will be required to determine their true relationship, but, in view of their small size and hard consistency, detailed investigation will not be easy.

PYRENOMYCETES

The Pyrenomycetes[1] include over 10,000 species; they possess a flask-shaped perithecium opening by a small pore, the ostiole, and containing an hymenium with parallel asci spread over the floor and lower parts of the sides. There are four alliances, the Hypocreales, Dothideales, Sphaeriales and Laboulbeniales. The Laboulbeniales are true Pyrenomycetes in that they produce regularly

[1] Seaver, 1909; Arnaud, 1920.

arranged asci and a perithecium opening by an ostiole, but they are distinguished by a number of special characters, some of which may be related to their peculiar habitat as external parasites on insects.

In the Dothideales the perithecia are always immersed in a stroma or cushion of fungal hyphae; in the Hypocreales and Sphaeriales they are sometimes isolated and free, sometimes sunk in the tissues of the host, sometimes embedded in a stroma. The perithecium is lined by delicate filaments, some of which, the **periphyses**, grow along and partly close the neck, and may protrude through the ostiole, while others, the paraphyses, are mingled with the asci in the venter of the fruit.

Accessory multiplication in these alliances is by chlamydospores, and by conidia which may be borne on free conidiophores or grouped in pycnidia. In some cases there is evidence that the so-called pycnidia are spermogonia and the cells they set free, spermatia; no case has been brought to light in which the latter still fulfil their function in connection with fertilisation, but neither have they been induced to undergo germination.

An archicarp has not been recorded in the Dothideales; in the Hypocreales and Sphaeriales the archicarp is of the coiled type found in *Eurotium* and in several of the Ascobolaceae; in most of the forms with free perithecia it is comparatively short and simple, in species with immersed perithecia it may be elaborately coiled, furnished with a many-celled trichogyne, and associated with the development of spermatia in spermogonia; in many cases it is known that the trichogyne does not function, and in several that the ascogenous hyphae develop from vegetative cells, and not from the archicarp. Finally, in *Xylaria* and other of the higher Pyrenomycetes, the archicarp is reduced to a short row of cells, sometimes known after its discoverer as Woronin's hypha, or, as in *Cordyceps*, no trace of an archicarp can be found.

The Pyrenomycetes do not seem to have given rise to any higher forms, some of their number have a greater vegetative development than any other Ascomycetes.

They may be subdivided as follows:

Wall of perithecium differentiated from stroma;

    Perithecium wall and stroma, if present, soft in
      texture, colourless or light coloured   HYPOCREALES

    Perithecium wall and stroma, if present, firm,
      leathery or brittle, dark in colour   SPHAERIALES

Perithecium always sunk in a stroma from the tissue
        of which its wall is not differentiated; colour of
        stroma black or dark brown   .   DOTHIDEALES.

Minute, external parasites on insects, perithecium
        borne on a receptacle which also bears append-
        ages, spores two-celled   LABOULBENIALES

HYPOCREALES

The Hypocreales are readily distinguished by the clear colour
and fleshy consistency of the perithecium or stroma. In most of
the Pyrenomycetes the colour is black or dark brown, here bright
red, yellow, purple and various pale shades are found; it is only
occasionally that so dull a tint as brown or dirty violet appears.

The asci contain usually eight, in some cases four, and in some
many spores. The spores are usually hyaline, but are dark coloured
in *Melanospora* and its allies; they are elliptical or filiform and may
be one or more celled.

There are some sixty genera of Hypocreales. In the simplest
forms a stroma is absent, and the separate perithecia may or may
not be partly sunk in the substratum; in others a fleshy stroma
appears and the perithecia are more or less embedded in it. In
the highest members the perithecia originate deep in the stroma
and remain immersed throughout their development. Upon these
characters the subdivision of the alliance is based:

Stroma absent, or when present with perithecia
    entirely superficial   NECTRIACEAE

Stroma forming a conspicuous matrix in which the
    perithecia are partially or entirely immersed   HYPOCREACEAE

NECTRIACEAE

Among the members of this family are a considerable number
of parasites; species of *Hypomyces*[1] and *Melanospora*[2] attack hy-
menomycetous fungi. In both genera a coiled archicarp has been
recorded, and sometimes a simple antheridium, but few details are
available. In *Hypomyces* the perithecia are free, in *Melanospora*
there is a filamentous stroma.

In *Nectria* (fig. 158) the usually red or yellow perithecia are
produced on a fleshy stroma of the same colour. The genus is

[1] Moreau, 1914.   [2] Kihlmann, 1885; Nichols, 1896.

large with some 250 species, of which *N. cinnabarina*, the commonest in Great Britain, occurs on the branches of deciduous trees. The mycelium from the germinating spores is unable to penetrate the bark of the host, and either enters through open wounds or spreads along the xylem elements from a dead region to the living tissues; as the mycelium grows, blocking of the wood causes wilting and death[1]. Meanwhile stromata appear; in the conidial stage they are bright pink and occur at all seasons on dead or living branches; perithecia are produced only in the autumn and winter and only after the tissues have been killed. They are

Fig. 158. *Nectria cinnabarina* (Tde.) Fr. on a fallen twig; *a*, conidial stroma; *b*, young perithecia; × 6; E. J. Welsford del.

deep red in colour, and are partly immersed in deep red stromata. When a perithecium is about to be formed a coil of hyphae larger than the other elements of the stroma appears a little below the surface, and probably represents the remains of whatever sexual apparatus originally gave rise to ascogenous hyphae.

Nectria galligena[2] is the cause of apple canker, the perithecia developing on withered apples and serving to tide the fungus over the winter; oogonial cells have been observed but degenerate early and the ascogenous hyphae arise from vegetative filaments.

Both species are examples of the rather numerous fungi which produce conidia during their parasitic phase, and ascospores only when the death of the host has rendered them saprophytic. Among other species of *Nectria* several are parasites on scale insects[3].

[1] Mayr, 1882; Line, 1922. [2] Cayley, 1921; Dillon Weston, 1925.
[3] Petch, 1921.

Among the Hypocreaceae *Polystigma*[1] is a small genus, the best known member of which, *P. rubrum*, develops on the leaves of *Prunus spinosa*, of *Prunus institia*, and of the cultivated plum, where it produces conspicuous orange, yellow, or scarlet stromata. Each stroma is the result of a separate infection and spreads over only a small part of the leaf, so that, in autumn, when the leaves are shed, the host is freed from the disease. The fungus, however,
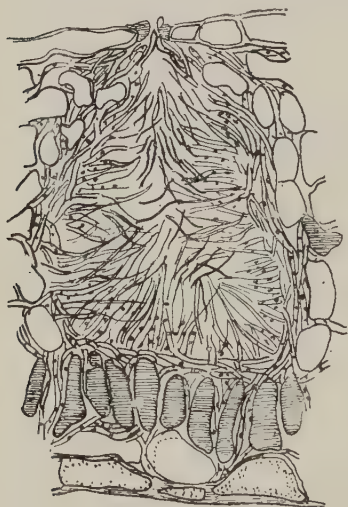
Fig. 159. *Polystigma rubrum* DC.; spermogonium, × 250; after Blackman and Welsford.

Fig. 160. *Polystigma rubrum* DC.; mature archicarp, × 800; after Blackman and Welsford.

hibernates in the fallen leaves, and next spring, unless these are destroyed, the ascospores mature, reach the young foliage, and cause fresh infections.

Within the leaf the hyphae ramify among the cells of the host, becoming especially massed in the intercellular spaces below the stomata and often pushing their way to the exterior between the guard-cells. Finally the stroma may extend from the lower to the upper epidermis and only a few isolated cells of the mesophyll be found in the infected region. During the summer, flask-shaped

[1] Fisch, 1882; Frank, 1883; Blackman and Welsford, 1912; Nienberg, 1914; Higgins, 1920.

spermogonia appear and open on the under side of the leaf, usually in the position of a stoma. The wall of the spermogonium consists of densely interwoven filaments and it is lined by thin, uninucleate, spermatial hyphae (fig. 159), from the ends of which spermatia are abstricted. The mature spermatium is a curved, filiform cell, containing a single, elongated nucleus. All attempts to bring about the germination of the spermatia have failed, and no relation of any kind has been demonstrated between them and the female organs; conse-

Fig. 161. *Polystigma rubrum* DC.; vegetative hyphae projecting through stoma above archicarp, × 900; after Blackman and Welsford.

quently their original use can be inferred only from their structure. Their small size, scanty contents, and large nucleus suggest that
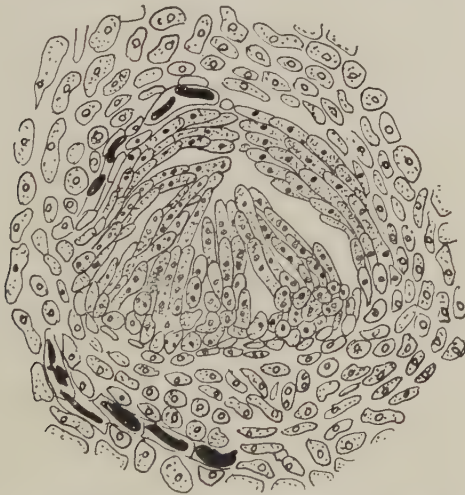
Fig. 162. *Polystigma rubrum* DC.; young perithecium; the ascogenous hyphae are not yet clearly distinguished, many of the nuclei are in pairs, the darkly stained remains of the archicarp are visible near the periphery; × 680; after Blackman and Welsford.

they are better constituted to act as agents of fertilisation than as a means of vegetative increase.

The archicarps originate as multinucleate hyphae which become

septate and elaborately coiled (fig. 160). Each usually appears separately below a stoma through which vegetative filaments project (fig. 161). The projecting filaments were at one time regarded as trichogynes, but no connection can be traced between them and the archicarps. The latter degenerate without giving rise to a sporophyte and the ascogenous hyphae are derived from the surrounding vegetative cells, among which the remains of the archicarp can sometimes be seen (fig. 162). There is some evidence that pseudapogamous fusions take place in the cells of the ascogenous

Fig. 163. *Polystigma rubrum* DC.; mature perithecium, × 270; after Blackman and Welsford.

hyphae before the appearance of asci. A perithecium (fig. 163) arises in the position of each archicarp.

In the genus *Podocrea* the stroma is erect and sometimes branched; in *Hypocrea* it is usually hemispherical or bolster-shaped; in both genera and their immediate allies the ascospores are two or more celled; most of the species occur saprophytically on wood or as parasites on the larger fungi. The systematic position of *Podocrea* has undergone some curious vicissitudes; in consideration of its form *Podocrea alutacea*[1] was first placed in the Clavari-aceae; later, when the perithecium-bearing head of the stroma had been recognised as pyrenomycetous, it was regarded as parasitic on its own stalk, which was classified as a *Clavaria* or as one of

[1] Atkinson, 1905.

the Geoglossaceae. Finally the upright stroma was grown in pure culture from the ascospores and thus shown to be a single fungus.

The species of *Epichloë* occur parasitically on the stems of grasses which become coated by the white or yellow stroma. During development oval conidia are produced, later the perithecia, which are completely immersed in the stroma, reach maturity. As in the remaining genera of the Hypocreaceae, the ascospores are filiform.

The genus *Cordyceps*[1] (fig. 164) includes about sixty species; these are mainly tropical parasites on insects, the bodies of which they transform into sclerotia. The peculiar appearance of these structures and of the stromata derived from them has given rise to curious views as to their significance and medicinal value. *Cordyceps sinensis*, for example, was a celebrated drug in the Chinese pharmacopoeia. The quaint belief that it was "a herb in summer and a worm in winter" may sufficiently account for the esteem in which it was held.

The ascospores are filiform and multicellular and, when shed, break up into their separate segments. The germ tubes from these or from the conidia penetrate the insect and cut off cylindrical cells which enter the blood stream and increase by yeast-like budding until the creature dies. A mycelium then appears and the formation of the sclerotium begins, while chains of conidia may be produced on subaerial conidiophores arranged in a parallel fascicle or coremium. The mature sclerotium is a compact mass of interwoven hyphae whose cells are rich in glycogen and oil; its development destroys the internal organs of the host, the skin alone remaining intact, so that the appearance of the insect is maintained. From this mummified structure the stromata emerge; they are pale or bright coloured, red in the best known British species, *C. militaris*, in others purple, flesh-coloured, lemon-yellow or brown. The perithecia (fig. 165) are embedded in the upper portion.

Two species, *C. ophioglossoides*[2] (fig. 164 *b*) and *C. capitata*, are parasitic on subterranean fungi of the genus *Elaphomyces*; in contrast to the forms on insects, they do not produce true sclerotia.

The species of *Claviceps*, like those of *Cordyceps*, possess filiform ascospores, they also form sclerotia from which stromata arise.

[1] Berkeley, 1843; Tulasne, 1861–5; Massee, 1895.   [2] Lewton-Brain, 1901.

The genus includes six species parasitic on members of the Gramineae. The best known is the almost cosmopolitan *C. purpurea*, the ergot, on rye and other grasses.

The ascospores germinate on the flowers of the host; and the

Fig. 164. *a, Cordyceps militaris* (L.) Link; *b, Cordyceps ophioglossoides* (Ehrh.) Link; after Tulasne.

mycelium ramifies in the ovary, ultimately forming a sclerotium; meanwhile hyphae reach the exterior, bud off conidia to which the generic name *Sphacelia* was formerly applied, and excrete a sweet fluid; this attracts insects which carry the conidia with them to other flowers where they may germinate and produce infection. On the completion of the conidial stage the sclerotia become dark purple or bluish-black in colour. If they fall to the ground or are

sown with the seed they give rise next spring to numerous stromata with violet stalks and rose-pink heads in which the perithecia are immersed.

During the formation of the perithecium a coenocytic antheridium and oogonium are stated to develop[1] from a common branch and undergo fusion; they appear to degenerate without giving rise to ascogenous hyphae; these, as in *Cordyceps*, are derived from the vegetative cells.

The sclerotia are well supplied with reserve materials and contain ergotic acid, a narcotic which diminishes reflex excitability; sphacelic acid, a poison inducing gangrene and, in large doses, cramp and tetanus of the uterus; and an alkaloid, cornutin, which causes contraction of the uterus and is, for this reason, of medicinal value.

Owing to the presence of sphacelic acid the sclerotia, if included in the grain used for bread making, are a cause of serious disease.

Fig. 165. *Cordyceps Barnesii* Thwaites; perithecia, × 170; after Massee.

When the grain was less carefully purified than at present, the inhabitants of whole districts sometimes became afflicted with gangrene. Moreover, when the sclerotia are eaten by sheep or cows, cornutin is liable to cause abortion, and many local traditions as to the prevalence of abortion in certain fields or byres are probably due to this cause.

DOTHIDEALES

The Dothideales are a small alliance of some four hundred species included in a single family, the Dothideaceae. Except for *Phyllochorella oceanica*[2], parasitic on the gulf weed, *Sargassum*, they are parasites and saprophytes on the leaves or stems of higher plants, forming stromata usually below the epidermis and finally

[1] Killian, 1919.　　　　　　[2] Ferdinandsen and Winge, 1920.

exposed by its rupture. The perithecia are immersed and are without definite walls so that the asci develop in mere cavities in the stroma, which, however, have the globose form of a perithecium and are lined by cells rather smaller than those of the surrounding mycelium.

In *Dothidea* the stromata form black, projecting cushions; in *Plowrightia* they run together in masses. *P. morbosa* attacks species of *Prunus*, especially the cherry and plum, and produces the swelling and deformation of the branches.

SPHAERIALES

The Sphaeriales are distinguished by the dark colour and membraneous, corky, or carbonaceous texture of their perithecia, and of their stromata if present. They include considerably over 6000 species and new species are constantly brought to light, so that further search, especially for tropical forms, will no doubt greatly increase their number. Not only the number of species, but also the number of individuals, is very considerable; the majority are saprophytes and serve a useful purpose in bringing about the first stages of decay in such resistant materials as wood or straw. They greatly outnumber the Hypocreales and Dothideales, and it is from their black or brown colour and often charred appearance that the name Pyrenomycetes is derived.

The perithecia of the simplest forms are borne singly, free or partly embedded in the substratum; from these may be traced a series of intermediate forms culminating in the elaborate stromata and sunken perithecia of the highest species. There is, indeed, a marked parallelism between the Hypocreales and Sphaeriales and it is by no means clear that the colour and texture of the stromata and perithecial walls are sufficiently important as criteria of relationship to justify the separation of the two alliances. Considerably more knowledge will, however, be required before a natural system of classification can be elaborated. In the meantime the subdivisions of the Sphaeriales rest on the form of the ostiole, the colour and septation of the spores, and the structure and development of the stroma. As in the Hypocreales accessory fructifications of several kinds may be present.

In the first eight families the perithecia are more or less free,

though they may be partly sunk in the substratum, or in a weft of hyphae, or may be seated on a definite stroma. In the remaining ten families the perithecia are immersed either in the substratum or in a stroma which may attain considerable elaboration.

The most important of the eighteen families may be distinguished as follows:

Perithecia free

Peridium membraneous	
Ostiole beset with long hairs often elaborately coiled or branched	CHAETOMIACEAE
Ostiole without long hairs, mainly coprophilous	SORDARIACEAE
Peridium leathery or carbonaceous	
Short neck	SPHAERIACEAE
Long, sometimes filiform neck	CERATOSTOMATACEAE

Perithecia embedded in substratum

Perithecia immersed, upper part free	
Ostiole round	AMPHISPHAERIACEAE
Ostiole elliptical	LOPHIOSTOMATACEAE
Perithecia completely immersed, ostiole only projecting	
Peridium membraneous or leathery, neck short	
Paraphyses absent	MYCOSPHAERELLACEAE
Paraphyses present	PLEOSPORACEAE
Peridium leathery or carbonaceous, neck long	GNOMONIACEAE

Perithecia embedded in stroma

Stroma developed within substratum, differentiated from it	VALSACEAE
Stroma free, ascospores dark brown	XYLARIACEAE

CHAETOMIACEAE

The members of the Chaetomiaceae occur on straw, paper, dung, and other waste materials; they possess free, thin-walled perithecia beset with characteristic long hairs (fig. 166), which are often branched or coiled. On these hairs, or on the hyphae of the mycelium, conidia may be produced. An ostiole is lacking in *Chaetomium fimeti*, in the remaining species it is present and the perithecium is of the usual flask shape (fig. 168).

In all species studied the archicarp[1] arises as a coiled branch (fig. 167), and divides into several cells; there is no sign of an antheridium.

The ripe spores are shed into the cavity of the perithecium and do not reach the exterior immediately on leaving the ascus.

[1] Zopf, 1881; Oltmanns, 1887; Vallory, 1911; Page, 1925.

SORDARIACEAE

The members of the Sordariaceae[1] are mainly coprophilous; their perithecia are for the most part free and superficial, but are

Fig. 167. *Chaetomium Kunzeanum* Zopf; archicarps; after Oltmanns.

Fig. 166. *Chaetomium pannosum* Wallr.; × 50; W. M. Page del.
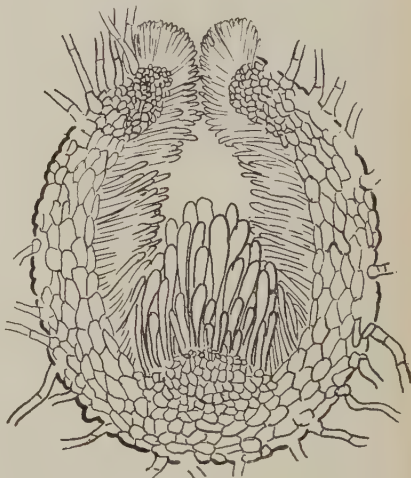
Fig. 168. *Chaetomium globosum* Kunze; perithecium, × 200; after Zopf.

sometimes so deeply sunk in the substratum that little more than the neck is to be seen. The genus *Hypocopra* is exceptional in possessing a small stroma in which the perithecium is immersed,

[1] Woronin, 1886; Lewis, 1911.

but it resembles the sordarias in other characters. The Sordariaceae differ from the Chaetomiaceae in not bearing long hairs around the ostiole (fig. 169), and from the Sphaeriaceae in the habitat and type of spore as well as in the texture of the peridium.

Fig. 170. *Podospora anserina* (Rabh.) Wint.; *a*, very young archicarp; *b*, older archicarp, × 400; after Page.

Fig. 169. *Sordaria* sp.; ascocarp in longitudinal section showing asci, paraphyses and periphyses, × 400.

The young perithecia are globose with plentiful secondary mycelium (fig. 172). The commonest type of archicarp is a stout, coiled, septate hypha (fig. 170), which soon becomes surrounded by vegetative filaments, making the details of its subsequent development difficult to determine; in *Sporormia*[1] longitudinal as well as transverse septa appear in one or more of

[1] Dangeard, 1907.

the cells, so that a small mass of true tissue is formed (fig. 171).
An antheridium has not been recorded in any of the Sordariaceae

Fig. 171. *Sporormia intermedia* Auersw.; initial cells of perithecium;
after Dangeard.

nor is it known whether any pseudapogamous process occurs, so
that the homologies of what is quite possibly a vestigial structure
are not easy to determine.

Fig. 172. *Sordaria Brefeldii* Zopf; group of three young perithecia showing
development of secondary mycelium, × 200.

In several of the Sordariaceae each ascospore is surrounded by
a layer of mucilage; in others one or more appendages[1] (fig. 173)
are produced. These may be gelatinous and derived partly or
wholly from the epiplasm, apparently much as the ordinary thick-
ening of the spore coat is derived, or they may show a lumen
continuous with that of the young spore. In the latter case they
are at first rich in cytoplasm, but later most of their contents pass

[1] Wolf, 1912.

into the main portion of the spore which becomes ovoid, and the
appendages are cut off by a wall. Both forms of appendage may
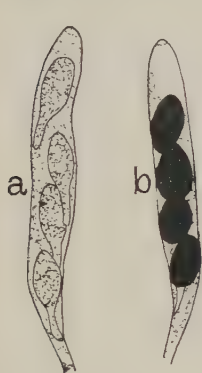
Fig. 173. *Podospora anse-
rina* (Rabh.) Wint.; four-
spored ascus, *a*, young,
b, older, showing spores
with appendages; × 280;
after Page.
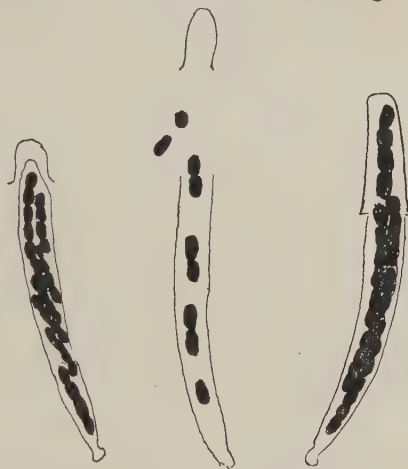
Fig. 174. *Sporormia* sp.; asci showing dehiscence
by means of a cap, × 335; W. M. Page del.

occur in the same spore. They are sometimes hooked and, be-
coming twisted together, serve to attach the spores one to another;

the uppermost appendage ap-
pears, in some cases at any rate,
to become fastened to the tip of
the ascus, so that they are carried
up when the ascus elongates.
The ascus usually opens by a lid,
but *Sporormia* is again exceptional
in the separation of a thimble-
shaped cap (fig. 174).

Fig. 175. *Sordaria fimicola* (Rob.)
Rabh.; germinating spores; × 400;
after Page.

    In the germination[1] of the asco-
spore part of the contents emerge
through a small aperture in the thick coat and form a swelling
(fig. 175) from which the first cells of the mycelium grow out.

SPHAERIACEAE

    The perithecia of the Sphaeriaceae are superficial, and borne
singly or in groups; the peridium is leathery or carbonaceous; it may
be smooth or beset with hairs; the neck of the perithecium is short.

[1] Page, 1925.

PYRENOMYCETES

Most of the species are saprophytes on plant remains, often on wood, but *Coleroa* (fig. 176) is parasitic on the leaves of *Potentilla*, *Rubus* and other angiosperms, and *Rosellina quercina*[1] attacks the roots of oak seedlings, entering the cells of the cortex and pith and forming interwoven strands of hyphae which grow out to infect neighbouring oak plants. This fungus may form black, chambered sclerotia in the cortex of the host root; multiplication is by conidia formed in summer at the surface of the soil, and later by asco-spores produced in perithecia. The formation of the peri-

Fig. 176. *Coleroa Potentillae* (Fr.) Wint.; perithecia, × 190.

thecium is initiated by the appearance of a pair of thick hyphae rich in contents, but their subsequent behaviour has not been determined, and no details of development are known either here or in other members of the family.

CERATOSTOMATACEAE

The Ceratostomataceae resemble the Sphaeriaceae in most of their characters; they are distinguished by the elongated neck of the perithecium, which is often drawn out to form a delicate, hair-like process.

In *Ceratostomella fimbriata*[2], the fungus of black rot on sweet potatoes, the archicarp consists of a basal cell and an oogonium prolonged into a trichogyne without a dividing wall; there is also an elongated antheridium. The male nucleus passes into the oogonium and unites with the female nucleus, the single, large, fusion nucleus being visible for some time after fertilisation. Rapid division then ensues and pairs of daughter nuclei enter the ascogenous hyphae and later fuse in the ascus.

The method of liberation of the spores through the long neck in this family presents an interesting problem.

[1] Hartig, 1880.   [2] Elliott, 1925.

In the Amphisphaeriaceae the young perithecium is sunk in the substratum; as it matures it becomes more or less free, though, in contrast to the condition in the Sphaeriaceae and Ceratostomataceae, its base is always immersed.

In *Strickeria*[1], a genus characterised by muriform spores, the perithecium originates from a cell which divides in more than one
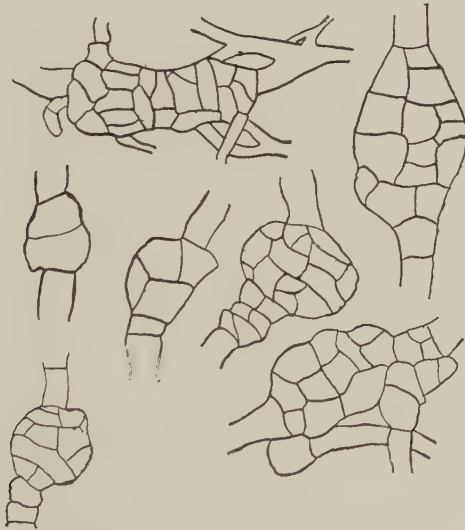
Fig. 177. *Strickeria* sp.; initial cells of ascocarps; after Nichols.

plane (fig. 177), as in *Sporormia*. The resultant parenchymatous mass appears to give rise to the perithecial walls as well as to ascogenous hyphae.

LOPHIOSTOMATACEAE

The perithecia are borne singly; during development they are embedded in the substratum, they may remain so or become partly free at maturity. There is no stroma; the peridium is black and brittle. The Lophiostomataceae are distinguished from neighbouring families by the form of the ostiole, which is very large and laterally compressed, so that in external appearance they

[1] Nichols, 1896.

approach certain of the Hysteriales which they also resemble in their habitat on vegetable remains such as wood and bark. None of the species has been investigated in detail.

MYCOSPHAERELLACEAE

The members of this family are parasitic, some on algae, some giving rise to various forms of leaf spot. The perithecia develop either under the cuticle or beneath the epidermis, breaking through at maturity; except in the genus *Stigmatea*, paraphyses are not developed. In several cases the formation of the perithecia is preceded by a conidial stage.

Mycosphaerella nigerristigma[1] forms pycnidia on the living leaves of *Prunus pennsylvanicae* and perithecia after the leaves have fallen. A trichogyne like that of *Polystigma* has been recorded; it degenerates, leaving a basal cell, but whether this functions is not known. An oogonium, a septate trichogyne and spermatia have also been described in *M. Bolleana*[2] on the leaves of *Ficus carica*; and in *Stigmatea Robertiani*[3], on *Geranium*, attention has been called to certain swollen cells below the hymenium which are stated to have a sexual significance.

PLEOSPORACEAE

The members of the Pleosporaceae are saprophytes or, in a few cases, parasites, for the most part on seed plants, but in some instances on Pteridophyta, Bryophyta, Lichenes, or Algae. The perithecia are immersed in the substratum, the ostiole only projecting, but they may become exposed by the rupture of the covering tissues. The peridium is leathery or membraneous.

Fig. 178. *Pleospora* sp.; germinating spores, × 500.

The genus *Pleospora*[4] includes some 225 species, several of which occur on graminaceous crops and other grasses where they show biologic specialisation. *Pleospora herbarum* is a facultative parasite upon the leaves of angiosperms; the perithecium is developed from

[1] Higgins, 1914.   [2] Higgins, 1920.
[3] Killian, 1922.   [4] Diedicke, 1902.

a mass of parenchyma, the asci originating from the same cells as the paraphyses. The ascospores (fig. 178) are muriform. Multicellular conidia on branched conidiophores are also produced. In some of the species of this genus and of the closely related *Pyrenophora* the ascus possesses a double wall; when dehiscence is about to occur the outer wall is ruptured and slips down to form a ring about the middle of the ascus[1], the inner wall opens just above this ring, and the spores are shot out with considerable force.

There are some fifty species of *Venturia*, several of which are parasitic on leaves; the perithecium is immersed and the large ostiole beset with stiff hairs. A coiled archicarp and an antheridium have been recorded for *V. inaequalis*[2] and the passage of male nuclei through the trichogyne reported. The conidial stage of this species, known as *Fusicladium dendriticum*, attacks the fruits and vegetative organs of the apple in summer, while the stromata are found in autumn on the fallen leaves and give rise to perithecia in the following spring.

Fig. 179. *Leptosphaeria Lemaneae* (Cohn) Brierley; transverse section through thallus of *Lemanea*, showing perithecium, × 125; after Brierley.

Leptosphaeria includes some 500 species characterised by the papillate or conical ostiole, usually free from hairs. The majority are saprophytes on plant remains, some are parasites on land plants, and *L. Lemaneae*[3] (fig. 179) infects the thallus of species of the red alga, *Lemanea*.

GNOMONIACEAE

The Gnomoniaceae are for the most part saprophytic on the leaves or other parts of land plants. The perithecia are embedded in the substratum, from which their long necks project. The asci

[1] Atanasoff, 1919.   [2] Killian, 1917; Frey, 1924.
[3] Woronin, 1886; Brierley, 1913.

are characterised by their thick apices through which a canal allows the exit of the spores. The spores are hyaline; paraphyses are not usually developed. The family differs from the Pleosporaceae in the long neck of the perithecium and the thickened tip of the ascus. There is no stroma, and this fact, as well as the dark colour, distinguishes *Gnomonia* from the similar genus *Polystigma* among the Hypocreales.

Gnomonia erythrostoma[1] is the cause of an epidemic disease known as cherry leaf-scorch, which attacks the foliage of *Prunus avium* and of varieties of the cultivated sweet cherry. The mycelium ramifies in the leaf and runs back to the base of the petiole where it prevents the formation of the absciss layer. In consequence the infected leaves do not fall, as in *Polystigma*, but remain hanging on the branches; they are the only source of infection in the following summer and their destruction is a sure means of checking the disease.

Infection usually takes place in June; towards the end of August spermogonia appear and form spermatia similar to those of *Polystigma*. At about the same time coiled archicarps are differentiated under the lower epidermis of the host leaf; their lower cells contain dense cytoplasm and large nuclei, and presumably represent an oogonial region, but it is doubtful whether they give rise to ascogenous hyphae. Four chromosomes are present in the ascus nuclei and there is evidence of only one reduction, so that the fungus is in all likelihood completely apogamous.

VALSACEAE

The perithecia of the Valsaceae are frequently produced in compact groups on black stromata from which their long necks alone project. The stroma is developed within the substratum from which it is not always completely differentiated; it is very variable in form, sometimes indicated only by a black stain on wood or bark and by a black margin, sometimes extended as a thin black layer over a considerable area and ending irregularly, sometimes, as in species of *Valsa*, forming black cushions which break through the bark of the substratum. Conidia are often present, borne on free conidiophores or produced within pycnidia.

[1] Frank, 1886; Brooks, 1910; Dowson, 1925; Likhité, 1925.

The genus *Valsa* includes some 400 species, for the most part saprophytic on wood and other resistant materials, and *Diaporthe* a rather larger number, the majority of which infect living plants. In one of the latter, *Diaporthe perniciosa*[1], a coiled, multicellular
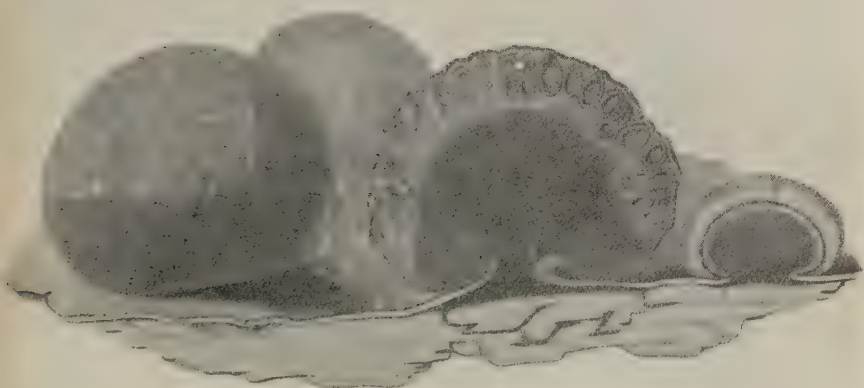
Fig. 180. *Hypoxylon coccineum* Bull.; the smallest stroma bears conidia, the others perithecia; after Tulasne.

archicarp has been recorded, but its relation to the ascogenous hyphae is not known.

XYLARIACEAE

The Xylariaceae occur chiefly on wood; they constitute the highest development of the Sphaeriales and are characterised by the free, superficial stroma, though a few, such as species of *Hypoxylon*, have stromata partly sunk in the substratum. The stromata show every variety of form, from a spreading crust, as in *Nummularia*, to the almost spherical cushions of *Daldinia* or *Hypoxylon* (fig. 180), and

[1] Cayley, 1923.
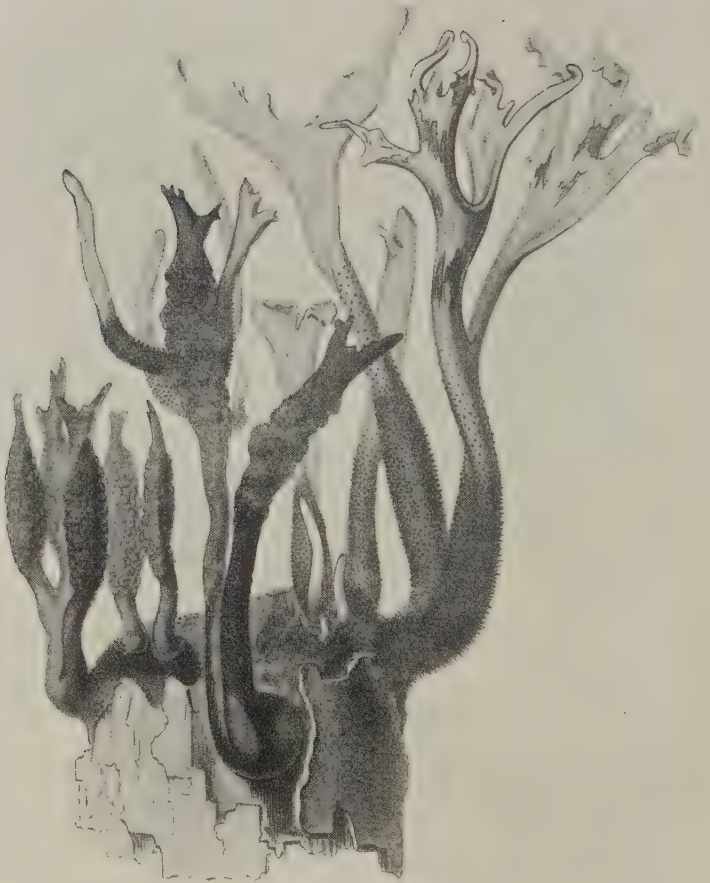
Fig. 181. *Xylaria Hypoxylon* Grev.; after Tulasne.

the erect, simple or branched expansions of *Xylaria* (fig. 181) and its allies. The perithecia are arranged just below and at right angles to the surface of the stroma; their development may be preceded by the formation of conidia, which often cover young stromata with a white or brown powder.

Poronia punctata[1] occurs on old horse-dung; the stromata are

Fig. 182. *Poronia punctata* (L.) Fr.; *a*, surface; *b*, lateral view; after Tulasne.

stalked, and expanded above into a cup or disc (fig. 182), which, in the earlier stages of development, is covered by a greyish-white film of conidia; later the ostioles of the numerous perithecia (fig. 183) appear as black dots scattered over the surface of the disc. The asci, when ripe, protrude through the ostiole, so that the spores are shed outside the perithecium. Before the conidia have

[1] Tulasne, 1861–5; Dawson, 1900.

Fig. 183. *Poronia punctata* (L.) Fr.; stroma cut across; after Tulasne.

Fig. 184. *Poronia punctata* (L.) Fr.; *a*, archicarp, × 275; *b* and *c*, young perithecia, × 205; after Dawson.

disappeared archicarps are developed among the vegetative fila-
ments as coils of deeply staining cells continued towards the
surface in the form of a slender trichogyne (fig. 184 a). It is clear
that the trichogyne does not function, as degeneration proceeds
from its base and not from its apex, as might be expected
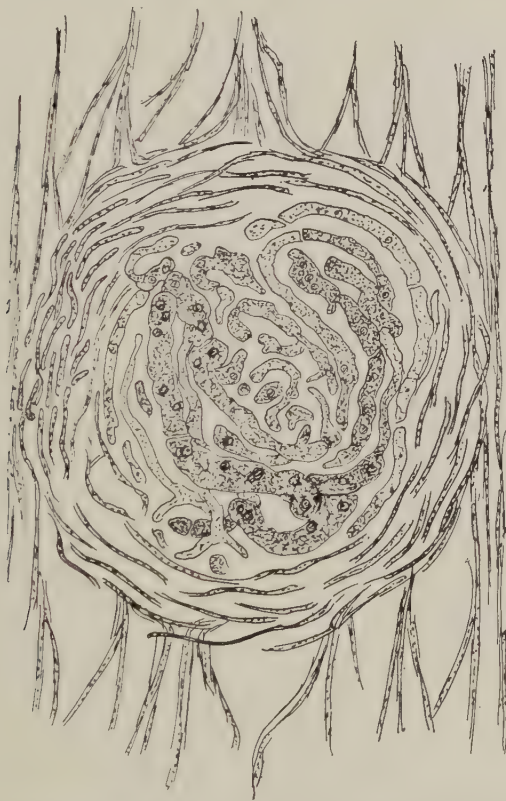
Fig. 185. *Xylaria polymorpha* (Pers.) Grev.; young perithecium, × 1000.

if a male nucleus were travelling down; the relationship of the
ascogenous hyphae to the oogonial region of the archicarp has not
been demonstrated.

In both *Xylaria*[1] and *Hypoxylon* the young stroma is covered
by a forest of conidiophores from which the small, oval conidia
are abstricted. In *Xylaria* these form a white coating in marked

[1] Freeman, 1910; Brown, H. B., 1913.

contrast to the exposed portions of the black stroma, and justify the name candle-snuff fungus applied to the commoner species. If the stroma of *Xylaria* or *Hypoxylon* is sectioned during the conidial stage, nests of small hyphae are found, and form the first indications of perithecia (fig. 185). Still earlier a stout hypha

Fig. 186. *Xylaria polymorpha* (Pers.) Grev.; archicarp embedded in stroma, × 1000.

Fig. 187. *Laboulbenia elongata* Thaxter; bicellular spore; after Thaxter.

with large nuclei, presumably an archicarp, is recognisable (fig. 186). In *Xylaria* it has not been shown to function, but in *Hypoxylon coccineum*[1] the development of ascogenous hyphae from its cells has been described.

LABOULBENIALES

The Laboulbeniales[2] include some 600 species, twenty-eight of which are British, arranged in over fifty genera. All are minute, external parasites on insects, chiefly on members of the Coleoptera.

[1] Lupo, 1922.
[2] Thaxter, 1896 i, 1908; Biffen, 1908; Faull, 1911, 1912; Maire, 1912, 1916; Hake, 1923.

They appear to do little injury to their host, inducing at most a slight irritation but never causing death; indeed, their own existence depends on the survival of the insect, since their life ends with that of their host. It is to the work of Thaxter that most of the existing knowledge of this group is due.

The Laboulbeniales are of simple structure and show an underlying similarity of type. In all cases the vegetative part consists of a **receptacle** (fig. 189), usually two celled, attached to the

Fig. 188. *Laboulbenia chaetophora*;   Fig. 189. *Laboulbenia triordinata* Thaxter;
young perithecium and trichogyne,   × 135; after Thaxter.
× 360; after Faull.

integument of the host by a blackened base or foot. From the receptacle grow out filamentous **appendages** on or among which the male organs are produced, and, with a few exceptions, the receptacle of the same individual also gives rise to a female organ from which a perithecium liberating ascospores is eventually developed. The fungus is covered by a thin, homogeneous membrane, which is exceedingly tough and impervious and is derived from the gelatinous coat of the spore; it efficiently protects the cells from desiccation. Within this coat the cells are uninucleate (fig. 188) with thick, laminated walls, sister cells being in communication by means of broad pits.

The spores are remarkably uniform throughout the alliance, being hyaline, fusiform or acicular, and almost always two celled (fig. 187). There is a gelatinous sheath, especially well-developed around the larger cell, which is towards the tip of the ascus, and is therefore destined, when the spore is discharged, to come in contact with the integument of the host. Here the gelatinous mass enables the spore to take up the oblique position in which germination occurs, and later gives its attachment a certain elasticity, so that it lies back along the body of a rapidly swimming host. In *Stigmatomyces* a short, pointed haustorium penetrates a little way into the chitinous covering of the insect, but it never reaches the subjacent tissues, and the suggestion has consequently been made[1] that the fungus may possess the power of

Fig. 190. *Zodiomyces vorticellarius* Thaxter; after Thaxter.

hydrolysing chitin and using it as food. On the other hand, species occurring on soft-bodied insects or on the soft parts of others exhibit a definite rhizoidal apparatus which enters the body of the host and doubtless absorbs food from the fluid materials in which it is bathed. Closely related species which do not penetrate the covering of the host differ not at all in their cell contents or mode of life from forms with rhizoids, suggesting that all alike are supplied by the circulatory system which, by diffusion or otherwise, nourishes in the living insect the structures on which they occur.

[1] Boedijn, 1923.

This inference is borne out[1] by the greater luxuriance of specimens growing near the circulatory centres or along the circulatory channels, even when attached to a chitinous structure.

The receptacle develops from the larger cell of the spore. It consists, in the simplest cases, of two superposed cells and, in monoecious forms, bears appendages terminally and the perithecium laterally. More rarely it consists of a greater number of

Fig. 191. *Ceratomyces rostratus* Thaxter; exogenous spermatia; after Thaxter.

Fig. 192. *Dimeromyces Africanus* Thaxter; compound spermatial organ; after Thaxter.

cells, attaining considerable complexity in *Zodiomyces vorticellarius* (fig. 190).

The appendages are filamentous and often elaborately branched. They bear the male organs, serve for the protection of the delicate trichogyne and may also facilitate fertilisation by holding water around the structures concerned. The first appendage is derived from the smaller segment of the spore, the later appendages arise from the receptacle.

The male elements are non-motile cells. In the simplest cases these are produced externally on the tips of more or less specialised branches (fig. 191); they are walled and seem to correspond exactly to the spermatia of other fungi, that is to say, they are antheridia

[1] Thaxter, 1914 i.

each reduced to a single, uninucleate cell, and carried by external agencies to the female organ. In *Coreomyces*, instead of the seg-

Fig. 193. *Stigmatomyces Baeri* Peyritsch; development of the perithecium; *a* shows the two-celled receptacle, a single appendage bearing five simple, endogenous spermatial organs, and the beginning of the perithecium; *b–i* indicate successive stages in the development of the perithecium; the trichogyne first appears in *d*; in *e*, spermatia are being shot out and some are attached to the trichogyne; in *i*, two of the four ascogenous cells are shown, with the superior sterile cell above them, and the primary and secondary inferior sterile cells below; after Thaxter.

ment of a branch becoming detached, its contents are extruded as a naked, uninucleate mass. This arrangement leads to more specialised endogenous organs which may be borne singly (fig. 193 *a–e*), or in groups (fig. 192). The naked mass of protoplasm may be

regarded as homologous with a spermatium, or the organ in which
it is produced may be looked upon as antheridial and the naked
mass itself as a non-motile male cell. In view of the close resem-
blance in other particulars between exogenous and endogenous
forms, the former hypothesis seems the more probable and the
term spermatium may conveniently be used.

The female organs are formed from the lower cell of the ger-
minating spore and are thus necessarily lateral, though this con-
dition is often obscured in the mature plant, where the ripening
perithecium may push the appendages
aside and take up an apparently terminal
position. Development is uniform for
the greater number of species and has
been fully described in *Stigmatomyces
Baeri*[1]. Here the lower cell of the recep-
tacle divides into two, and the upper
of these grows out (fig. 193 *a*) to form
the archicarp. It divides transversely,
the upper daughter cell gives rise to the
female organ, the lower or stalk cell of
the archicarp divides several times (fig.
193 *b*), and ultimately forms the double
wall of the perithecium, a function
shared by a complex of unrelated
hyphae in Ascomycetes of richer
development.
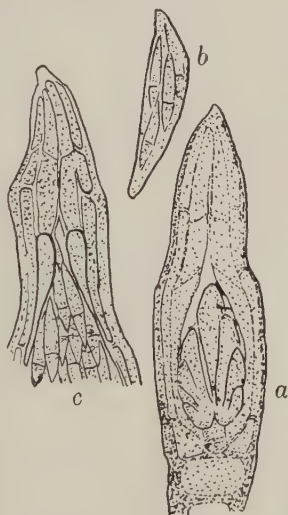
Fig. 194. *Stigmatomyces Baeri*
Peyritsch; *a*, young asci;
b, ascus containing four
spores; *c*, mass of spores in
perithecium; after Thaxter.

The upper cell divides, separating the
oogonium below from a cell above, which
divides again transversely to form the
two-celled trichogyne (fig. 193 *d, e*).

After the fertilisation stage the oogonium divides into three
(fig. 193 *g*) and then four superposed cells; the penultimate of
these, next but one to the trichogyne, divides longitudinally into
four ascogenous cells, two of which are shown in fig. 193 *i*, and
from these the asci bud out (fig. 194 *a*). The young ascus is bi-
nucleate; the nuclei fuse, and three nuclear divisions take place
in the usual way. As a rule, only four of the eight resultant nuclei
function, and four spores are produced. The lack of ascogenous

[1] Thaxter, 1896 i.

hyphae is doubtless due to restrictions of space; in other particulars the development of the female organ is closely comparable to the corresponding stages in the Erysiphaceae.
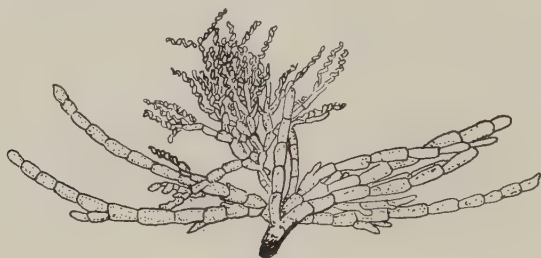
Fig. 195. *Compsomyces verticillatus* Thaxter; after Thaxter.

In *Stigmatomyces Baeri* the trichogyne is simple, but in many other Laboulbeniales it undergoes frequent septation and branches
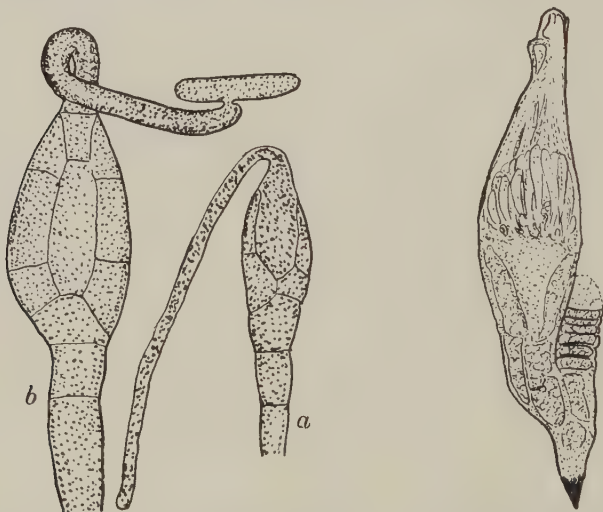
Fig. 196. *Zodiomyces vorticellarius* Thaxter; trichogyne *a*, before, and *b*, after, attachment of spermatium; after Thaxter.

Fig. 197. *Polyascomyces Trichophyae* Thaxter; after Thaxter.

freely (fig. 195). The apices of the branches alone are receptive and may be straight or spirally coiled.

In species with endogenous spermatia the latter are shot directly on to the trichogyne or carried to it by water which surrounds the fungi when their hosts are hiding in moist places. In *Zodiomyces*,

on the other hand, where the spermatia are formed externally, they fall from the parent branches to the cup-shaped receptacle and there appear to be sought by the trichogyne which is at first bent over (fig. 196 *a*), and later lifts itself when a spermatium has become attached (fig. 196 *b*).

Up to the present the cytology has been studied[1] only in two species of *Laboulbenia* and these, unfortunately, are both partheno-genetic, no spermatia being formed. Association takes place be-tween the oogonial nucleus and a nucleus from the lower cell of the trichogyne, but only one fusion, that in the ascus, has been seen. The haploid number of chromosomes is four.

There is some variation in different species in the number and arrangement of the ascogenous cells and asci. In *Polyascomyces* (fig. 197) as many as thirty ascogenous cells are formed, covering a basal area from which the numerous asci bud upwards.

The ascospores are usually disposed more or less definitely in pairs and members of a pair are discharged together and germinate side by side. In monoecious species one member of a pair may produce a smaller individual than the other, while in *Laboulbenia inflata* the atrophy of one at an early stage of development is a regular phenomenon. In *Stigmatomyces Sarcophagae* (fig. 198) the smaller individual is unisexual, producing only male cells, while the other is hermaphrodite.

In dioecious species, such as *Amorphomyces Falagriae* (figs. 200, 201), the paired spores are of different sizes (fig. 199); the smaller spore gives rise to a male individual, the larger to a female, so that their association insures the condition necessary for the perpetuation of the species. There is an obvious suggestion in these phenomena of a transition between the monoecious and dioecious conditions, but it is not clear in which direction the series should be read. It might be inferred that the male plant had become atrophied after the female had acquired spermatial organs, or, on the other hand, that, as in many other groups of plants, a hermaphrodite condition was primitive and segregation a later development. Any light on the cytology of dioecious species should be of special interest.

The systematic relations of the Laboulbeniales are not easy to determine. They are pretty evidently monophyletic and are highly

[1] Faull, 1912.

Fig. 199. *Amorpho-myces Falagriae* Thaxter; paired spores; after Thaxter.

Fig. 201. *Amorphomyces Falagriae* Thaxter; male and female individuals, the latter with perithecium containing spores; after Thaxter.

Fig. 198. *Stigmatomyces Sarcophagae* Thaxter; male and hermaphrodite individuals, × 260; after Thaxter.

Fig. 200. *Amorphomyces Falagriae* Thaxter; male and female individuals; *a*, young; *b*, mature; after Thaxter.

specialised along lines appropriate to their peculiar habitat. The ascocarp is definitely pyrenomycetous, but the production of asci from the subterminal cell only of the row formed after fertilisation recalls the Erysiphales, while the endogenous male element differs from anything found elsewhere among the fungi. The general inference is that the Laboulbeniales were derived from an ancestor already definitely ascomycetous but not otherwise highly specialised and that they have undergone considerable modification since branching off from the main line. It might be hazarded that the separation took place somewhere between the level of the Erysiphales and that of the lower Pyrenomycetes, while the ancestors of the latter still showed normal sexuality.

The Laboulbeniales are divided into three families, which, however, need not be separately considered here:

Spermatia endogenous
 Borne in compound organs PEYRITSCHIELLACEAE
 Borne in simple organs   LABOULBENIACEAE
Spermatia exogenous   CERATOMYCETACEAE

BASIDIOMYCETES

The Basidiomycetes include over 13,000 species possessing a well-developed mycelium which, among higher forms, builds up an elaborate fruit body, or **sporophore**, such as may be observed in the toadstools, bracket-fungi and puffballs.

The Basidium. Basidiomycetes are characterised by the fact that their principal spores, the basidiospores, are borne externally on the mother cell, or basidium. The young basidium contains two nuclei; these fuse; the fusion nucleus divides, providing the nuclei of the spores; the spore is formed at the end of a stalk, the sterigma, through which the nucleus passes from the basidium to enter the developing spore. Two successive divisions in the basidium constitute a meiotic phase. In the Autobasidiomycetes the basidia are without septa, and the spores are regularly four in number for each basidium (fig. 202). In the Protobasidiomycetes the basidium is divided into four cells, each of which gives rise to a single spore; the walls are transverse in the Uredinales and Auriculariales, longitudinal or oblique in the Tremellales. In the Hemibasidiomycetes septa may or may not be present in the basidium, but the fusion nucleus divides more than twice, and more than four spores are produced.

In several of the Uredinales and in *Sirobasidium* among the Tremellales the basidia are developed in chains, in other cases they are borne singly. In the Ustilaginales and in most of the Uredinales the contents of the basidium are at first enclosed in a thick wall, forming the **brand spore** or **teleutospore cell**, which becomes detached, serving as an additional means for the distribution of the plant; later the contents are extruded as a thin-walled **promycelium** on which the basidiospores are produced. In other Basidiomycetes the basidia are thin-walled throughout their development and give rise to spores while still attached to the mycelium.

The Basidiospores. The basidiospores are unicellular, round or oval in shape, usually with a smooth, rather thin wall. Echinulate spores occur in a few species, and in many families, especially among gill-bearing fungi, dark or bright coloured spores are common.

In a considerable number of genera accessory spores are also produced.

Sexual Reproduction. So far as is at present known there is
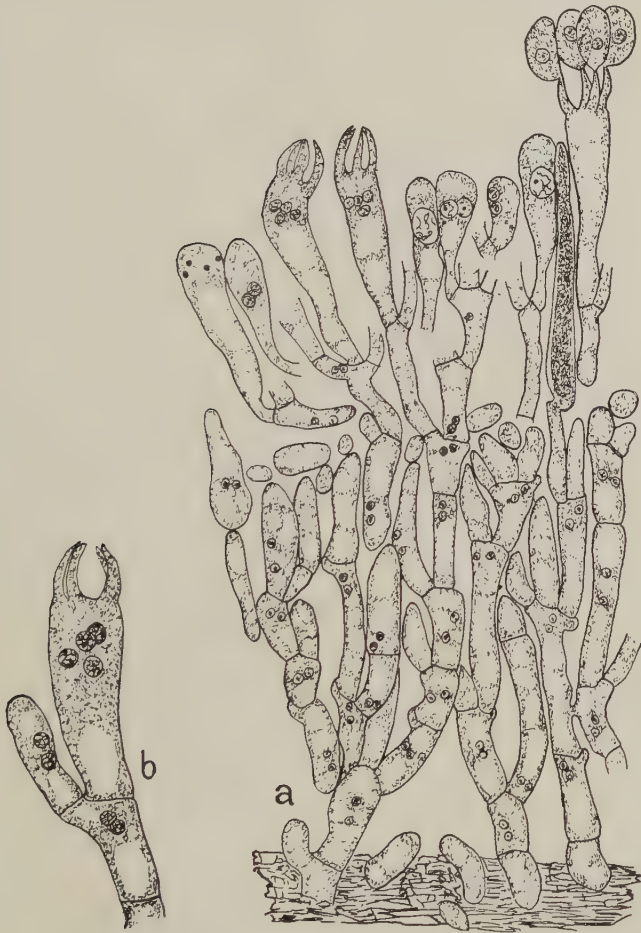
Fig. 202. *Hypochnus subtilis* Schroet.; *a*, hymenium of binucleate cells bearing basidia; *b*, a young, binucleate basidium, and an older one in which the fusion nucleus has divided to form the four spore nuclei and the sterigmata are growing out; after Harper.

no member of the Basidiomycetes in which normal fusion of male and female elements takes place; in the Uredinales sexual organs are still developed, though the antheridium no longer functions

and the male nucleus is replaced in the oogonium by a vegetative nucleus or the nucleus of another female organ. These nuclei do not fuse, but, as is usual with nuclei enclosed in the same cell, divide simultaneously, one descendant of each passing into each daughter cell, so that in due course a mycelium of binucleate cells is developed, to the paired nuclei of which the term **synkaryon** is applied. The conjugate condition comes to an end with the formation of the basidium, in which the paired nuclei fuse in preparation for the inception of meiosis. The union of the nuclei thus takes place in two stages, nuclear association being separated by a longer or shorter series of vegetative divisions from nuclear fusion, and the sporophyte, or diplophase, showing paired nuclei instead of nuclei with the double number of chromosomes. The postponement of nuclear fusion, though not unknown in other plants and animals, may probably here be regarded as indicating a degeneration of the sexual process.

In the remainder of the Protobasidiomycetes, in the Hemi-basidiomycetes and in the Autobasidiomycetes sexual organs are not found, but, as in the rusts, the young basidium and the cells of some part of the mycelium are constantly binucleate, and nuclear fusion occurs during the development of the basidium. The binucleate condition in the Hemibasidiomycetes arises at an early stage, when the basidiospores or their products become associated in pairs, and the nucleus of one passes into the other. In the Autobasidiomycetes, on the contrary, a considerable mycelium of uninucleate or multinucleate cells may be formed on the germination of the basidiospore; between the cells of such mycelia anastomoses are common, and in this way nuclei from different cells are brought together and a synkaryon formed. In most of the cases examined the basidium is the terminal segment of a filament of binucleate cells.

With this binucleate condition is associated the presence of clamp connections (figs. 202, 203) between adjacent cells. The formation of the clamp connection[1] takes place concurrently with the deposition of a cell wall and in connection with the conjugate division of a synkaryon. When division is about to begin, a beak or projection is put out from the cell, and, curving downwards, fuses with it again. Meantime the upper of the two nuclei approaches

[1] Kniep, 1915, 1916, 1917; Bensaude, 1918.

the beak, while the other remains in the parent hypha. Both
divide (fig. 203 *a, d*), and a daughter nucleus, passing through the
beak, lies near the daughter of the other member of the syn-
karyon (fig. 203 *b*). Cell walls are formed both across the beak and
across the original cell, each running at right angles to one of the

Fig. 203. *Collybia conigena* (Pers.) Quél.; *a, b,* secondary mycelium with clamp
connections, × 600; *Corticium serum* (Pers.) Fr., *c,* the same, × 600; *Armil-
laria mucida* (Schrad.) Quél.; *d,* paired nuclei dividing before the basidium is
cut off, a clamp connection in process of formation; *e,* young, binucleate
basidium borne on a hypha showing clamp connections; all after Kniep.

spindles of the synkaryon. The result of this somewhat complicated
process is that each of the new cells is binucleate. Such cells make
up the **secondary mycelium**[1], in contrast to the **primary myce-
lium**, in which binucleate cells and clamp connections are not
observed. In several species the lower parts of the sporophore

[1] Cf. p. 130.

consist of uninucleate and multinucleate cells, the synkaryon appearing first in the neighbourhood of the fertile region[1]; in many others it is from the secondary mycelium that the whole sporophore is produced.

This is the case in *Coprinus fimetarius*, *C. radians* and other species[2] in which secondary mycelium cannot normally be obtained in culture from a single spore, but arises when two appropriate strains of primary mycelium are brought into contact, the anastomoses from which the synkaryon originates taking place between them. Such primary mycelia are not wholly incapable of forming sporophores, but, when they do, there is no fusion in the basidium and the spores produced are of only one strain. Further, a monosporous culture may spontaneously become diploid[3], even after remaining for weeks in the primary state.

In several species matters are less simple, since more than two strains exist[4], and each is capable of forming secondary mycelium only with a limited number of other strains. This is the case in *Aleurodiscus polygonus* and *Coprinus lagopus* in which four strains, *AB*, *ab*, *Ab* and *aB*, are present, secondary mycelium being developed only when the combination *AaBb* is obtained. It is possible by judicious manipulation to separate and germinate separately the four spores of a basidium, and to discover that the same basidium may give rise to all the four above-mentioned strains, one from each basidiospore. Moreover, while each normal fruit body has its own four strains, *AB* giving secondary mycelium only with *ab*, and *Ab* only with *aB*, each of the four may be perfectly fertile with several strains from another sporophore of the same species. In *Coprinus lagopus* twenty-four strains have in this way been recognised and larger numbers are found in other forms.

It seems clear that, in the case of the four characters represented by *A*, *a*, *B* and *b*, segregation takes place on Mendelian lines, and a normal sporophore can be produced only when all four characters are present, two, *A* or *a* and *B* or *b*, occurring in each primary mycelium. The condition has been interpreted in terms of sexual

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[1] Cf. p. 287.
[2] Bensaude, 1918; Kniep, 1920; Mounce, 1921–3; Vandendries, 1922–5; Newton, 1926.
[3] Vandendries, 1925 i, ii; Newton, 1926.
[4] Kniep, 1920–3; Hanna, 1925.

differentiation, the primary mycelium being here described as heterothallic, and the Autobasidiomycetes as possessing several sexes, the occurrence of each of which depends on at least two factors. In every other multicellular organism, however, sexual differentiation implies the presence of gametes or gametangia and only two sexes are known. It is therefore questionable whether the differences observed in basidiomycetous mycelia are indeed differences of sex, and it seems more appropriate to employ terminology which does not involve this assumption. The word heterothallic is convenient and, in its literal sense, not inaccurate.

The facts observed are capable of interpretation in terms of metabolism[1]. If the letters A, a, B, b be taken each to represent the power of accumulating some substance essential to sporophore formation, the limiting factors in a primary mycelium from an AB spore will be the insufficiency of substances a and b, while the product of an ab spore will be inadequately supplied with A and B. Fusions between the two, and it must be remembered that mycelial fusions take place with great readiness in fungi, would, on the above hypothesis, remedy the defects of both, and ensure the provision of material for sporophore formation. The spontaneous development of secondary mycelia in single spore culture, and the occasional formation of sporophores on primary mycelia, suggest that the needful substances may also be accumulated, perhaps more gradually, in the ordinary course of nutrition. A somewhat similar condition may exist in the ascomycetous genus *Glomerella*[2], where perithecia are but scantily produced except where two strains meet, and nutritive phenomena are sometimes associated with the development of the sexual organs[3] in *Saprolegnia* and elsewhere. The condition in the Basidiomycetes with many strains may well have arisen after normal sexuality had disappeared.

In the Hemibasidiomycetes also evidence of heterothallism has been found, but the condition there seems to be comparatively simple.

The Sporophore. The Hemibasidiomycetes and Uredinales are without exception obligate parasites, with a delicate, endophytic mycelium, and do not build a sporophore. In these respects they differ markedly from the Autobasidiomycetes, and even their general characters require separate consideration. In most of the

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[1] Gwynne-Vaughan, 1926.   [2] Cf. p. 131.   [3] Cf. p. 78.

Autobasidiomycetes the sporophore is large, often with a central stalk, the **stipe**, distinct from the **pileus**, or cap, and with the fertile region limited to the surface of teeth, or of **lamellae** or gills, or to the interior of deep pores or of closed chambers.

Phylogeny. Though showing less uniformity of structure than the ascus, the basidium possesses characters sufficiently well defined to indicate a common origin for the Basidiomycetes. Such an origin has often been suggested through the conidial forms of the Phycomycetes or Ascomycetes, but the regular fusion of two nuclei in the basidium followed by meiosis, and the regular production in the Proto- and Autobasidiomycetes of four basidiospores, point to the basidium as the tetraspore mother cell, or final cell of the sporophyte, and to the basidiospore as the first cell of the haploid generation. The association of nuclear fusion and reduction with the development of accessory spores would involve important changes of which we have no indication.

The ancestor of the Basidiomycetes must have been a simple, filamentous fungus, probably with functional sexual organs not unlike those of the rusts, but perhaps with an antheridium still remaining attached. There may have been a well-marked alternation of independent, filamentous generations, the gametophyte originating from a basidiospore, and the sporophyte from a zygote, which may possibly have been a thick-walled resting cell such as occurs among Archimycetes to-day. All speculations of this kind, however, in view of our lack of knowledge of intermediate forms, must be of the most tentative character.

The Basidiomycetes may be divided as follows:

Number of basidiospores indefinite	HEMIBASIDIOMYCETES
Number of basidiospores definite, usually four	
Basidia septate	PROTOBASIDIOMYCETES
Basidia continuous	AUTOBASIDIOMYCETES

HEMIBASIDIOMYCETES

The Hemibasidiomycetes include a single alliance, the Ustilaginales; they are characterised by the fact that more than four spores are produced on the basidium, which may be septate or continuous.

USTILAGINALES

The Ustilaginales, brand fungi, smuts or bunts[1] are an assem-
blage of some 400 species, obligate parasites on the higher plants,
giving rise in the tissues of the host to thick-walled, usually dark-
coloured resting spores, the **brand spores**, or teleutospores. These

Fig. 205. *Urocystis Fischeri*;
spore ball, one spore pro-
ducing basidiospores on a
promycelium, × 500; after
Plowright.

Fig. 204. *Ustilago Treubii* Solms; stem of
Polygonum with "fruit gall," nat. size; after
Solms-Laubach[2].

are developed in considerable quantities, either singly, in pairs, or
in clusters known as **spore balls**, and when ripe break through the
host tissue, forming a pustule or sorus. No distortion of the host
is caused during the period of vegetative growth, but in prepara-
tion for the formation of spores very marked hypertrophy may be
induced.

[1] Prevost, 1807; Berkeley, 1847 i; Tulasne, 1847, 1854; de Bary, 1853;
Fischer von Waldheim, 1867; Brefeld, 1883; Ward, 1888 i; Plowright, 1889;
Dangeard, 1894 i; Lutman, 1911; Killian, 1924.
[2] Solms-Laubach, 1886.

Ustilago Treubii, on the stem of *Polygonum chinense* in Java, is responsible for the appearance of elaborate galls (fig. 204) provided with vascular tissue and growing by means of a cambium; *Ustilago Maydis* produces whitish swellings and blisters, often as large as a fist, on the organs of *Zea Mays*; and *Urocystis Violae* deforms the stems and leaves of species of *Viola*. Several smuts form their spores in the ovary of the host, or infect the stamens, filling the anthers with brand spores and benefiting by the means of distribution provided for the pollen. *Ustilago antherarum* even induces development of the staminal rudiments in the pistillate
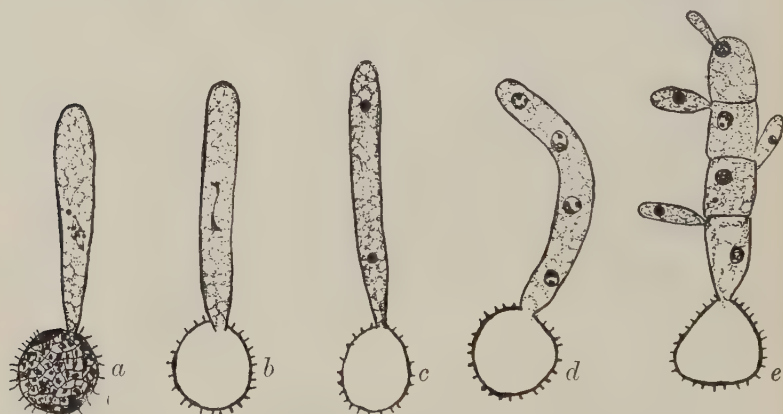
Fig. 206. *Ustilago Scabiosae* Sow.; development of basidium; after Harper.

flowers of *Lychnis dioica*; the stamens so formed undergo dehiscence as usual and differ from those of the male flowers chiefly in the presence of fungal spores instead of pollen in their anthers.

In all these species, and in most members of the alliance, spore formation is strictly localised, but in *Entyloma* and its allies spores may be formed in almost any part of the host.

The mature brand spore is uninucleate; it is surrounded by a delicate endospore and by an epispore which may be smooth or sculptured, and which usually contains pigment, giving the spore a black, brown or violet colour. Several may be grouped together to form a spore ball (fig. 205), with or without a coat of sterile cells.

On renewal of growth the brand spore gives rise to a short tube, the

promycelium (fig. 206 *a*), into which its contents pass, the nucleus undergoing at least two divisions; the promycelium in turn produces a number of basidiospores, or sporidia. The promycelium may be unicellular at first, bearing a bunch of spores at its apex (figs. 205, 207), or multicellular, usually four-celled, forming one or more basidiospores from each cell (fig. 206 *e*).

The nucleus of the parent cell does not travel into the basidiospore, but divides, sending one daughter nucleus into the spore, while the other, remaining in the basidium, may divide again and thus furnish nuclei for successive spores.

Under suitable conditions the basidiospores are cut off in considerable numbers. They may further multiply by budding, giving rise to conidia, or a delicate mycelium may be formed from which conidia are abstricted as in *Tilletia*. These

Fig. 207. *Tilletia Tritici* (Bjerk.) Wint.; *a*, basidium thirty hours after rupture of brand-spore; *b*, after conjugation of basidiospores; × 300; after Plowright.

changes occur in nature in the damp, manured soil of the fields.

During their development the cells of the basidium, the basidiospores or the conidia may become united in pairs (fig. 208) by means of a tube put out by one or both participants; the growth of these tubes is accurately directed and appears to depend on a chemotropic stimulus. In *Ustilago antherarum* and other species two or more strains are present[1], and fusion is not indiscriminate but between cells of opposite strains. Sometimes considerable numbers of spores or their products take part in a single group of fusions, and spores of three or four species may be involved in the same group. Fusions occur with special readiness in the presence of an ample supply of oxygen or when food material is lacking; indeed the formation of strains between the constituents of which fusion does not occur may be induced by cultivation on media rich in albuminous compounds or under other appropriate conditions.

[1] Kniep, 1919, 1926; Dickinson, 1927.

In most cases the nucleus of one of the associated cells passes down the tube into the other, but does not fuse with its nucleus. Later both nuclei divide and a mycelium of binucleate cells is produced. It is on this mycelium that the infection of the host depends; it penetrates the tissues of the seedling, or even the developing parts of the mature plant, and is usually derived from spores which adhered to the seed coat. These may be destroyed by dipping the seeds into hot water or formalin solution before sowing.

Once in the tissues of the host the mycelium of binucleate cells penetrates in all directions, ramifying between the cells of the host
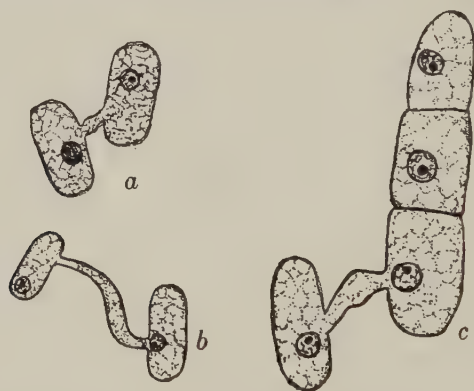
Fig. 208. *Ustilago antherarum* Fr.; *a* and *b*, conjugating basidiospores; *c*, conjugation between a cell of the basidium and a basidiospore; after Harper.

and sending haustoria into them. The internodes of the stem are traversed by long, unbranched hyphae, but in the nodes branching is frequent, and here also most of the haustoria are found. When the host is perennial the mycelium perennates with it, and, if the subaerial parts of the host die down in winter, remains quiescent in the stock till the growth of new shoots in spring gives a fresh opportunity for development.

Conidia on the parasitic mycelium are found in *Tuburcinia* and *Entyloma*, but are not of common occurrence in the alliance.

When the formation of brand spores is about to take place the mycelium becomes richly branched and often swollen and gelatinous; it may break into a number of short segments, the contents of each of which form a spore, or spores may be budded out

laterally. Where a spore ball is produced it may be furnished with an outer investment of sterile cells.

The young brand spore, like the cells of the mycelium from which it is derived, contains two nuclei (fig. 209). These fuse, so that the mature brand spore is uninucleate. The pairing of the nuclei, which begins with the association of the basidiospores, or of their conidia, is thus completed in the brand spore, which is homologous with the basidium of Autobasidiomycetes, the contents being extruded from the thick wall as a promycelium before the basidiospores are formed. There is here a definite alternation of a brief saprophytic gametophyte of uninucleate cells, and an extensive sporophytic mycelium of cells with paired nuclei, growing parasitically

Fig. 209. *Ustilago Carbo*; *a*, young, binucleate brand spores; *b*, older spores after nuclear fusion; after Rawitscher.

in the tissues of higher plants. In *Tuburcinia primulicola* the mycelia of both generations are parasitic and the condition therefore approaches that in the rusts.

The life history of the smuts would appear to be reduced rather than primitive, the conjugation of the basidiospores replacing a normal sexual process, but no information is available which justifies speculation as to what the original sexual apparatus may have been.

The Ustilaginales are divided into two families of about equal size which may be distinguished as follows:

<div style="text-align:center">

Basidia septate   USTILAGINACEAE
Basidia continuous   TILLETIACEAE

</div>

USTILAGINACEAE

Ustilago, with nearly 200 species, is the most important genus of the Ustilaginaceae. It is cosmopolitan, occurring on all sorts of host plants, and is characterised by the fact that its brand spores are borne singly, not in pairs or groups.

Ustilago Carbo[1] infects species of *Avena*, *Triticum* and *Hordeum*, the form on each host being biologically distinct. The brand spore develops readily in dilute nutritive solutions, forming a three- or four-celled basidium from which basidiospores may be abstricted in the usual way. More commonly, however, the basidia give rise, without spore formation, to branched mycelia, between the cells of which conjugation takes place. Conjugation may occur between adjacent cells by means of a short branch like a clamp connection (figs. 210 *a*, 211), or between unrelated elements by means of a
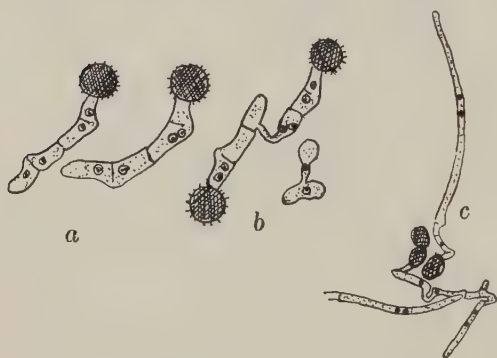
Fig. 210. *Ustilago Carbo*; *a*, *b*, conjugation; *c*, binucleate mycelium; after Rawitscher.
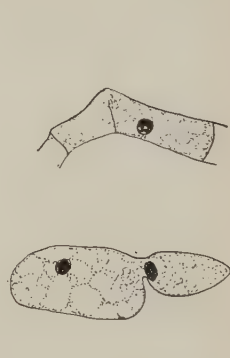
Fig. 211. *Ustilago Hordei*; conjugation; after Lutman.

tube (fig. 210 *b*). In either case the nucleus of one of the associated cells passes into the other, and the nuclei lie close together without fusion.

Ustilago Maydis[1], the smut of *Zea Mays*, produces considerable deformations containing the mass of gelatinous mycelium from which the brand spores are produced. When mature the spore mass swells, causing the rupture of the tissues, and the spores escape. The basidia abstrict uninucleate basidiospores; these multiply by budding, but do not conjugate, so that, when the host plant is infected, a mycelium of uninucleate cells is formed (fig. 212). The uninucleate condition is maintained until the hyphae begin to break up in preparation for spore formation; at this stage the walls between adjacent cells disintegrate (fig. 213),

[1] Rawitscher, 1912.

Fig. 212. *Ustilago Maydis*; *a*, basidiospores, × 540; *b*, mycelium of uninucleate cells, × 420; after Rawitscher.

Fig. 213. *Ustilago Maydis*; *a*, uninucleate cells before spore-formation; *b*, conjugation; *c*, young, uninucleate brand spores; after Rawitscher.
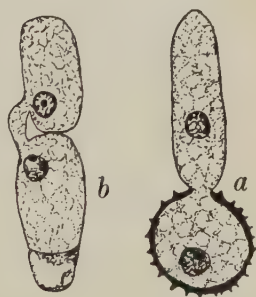
Fig. 214. *Ustilago antherarum* Fr.; *a*, development of brand spore; *b*, conjugation; after Harper.

the nuclei become associated, and soon fuse. Thus the young brand spore in *U. Maydis*, as in other species, contains two nuclei, and the mature spore a single nucleus, although the parasitic mycelium consists of uninucleate cells. A similar condition has been observed in *Ustilago Vaillantii*[1].

There is evidence[2] that, while some forms of *Ustilago antherarum* (fig. 214) have a life history similar to that of *Ustilago Carbo*,

Fig. 215. *Ustilago Tragopogi-pratensis* (Pers.) Wint.; conjugation and nuclear fusion; after Federley.

others are euapogamous, without any nuclear association or fusion. In *U. Tragopogi-pratensis*, on the other hand, fusion takes place between the basidiospores and the associated nuclei may unite at once[3] (fig. 215), so that the cells of the sporophytic mycelium have single, diploid nuclei.

TILLETIACEAE

The principal genera of the Tilletiaceae are *Tilletia*, *Entyloma*, *Tuburcinia*, *Urocystis* and *Doassansia*. They all show a basidium which is at first continuous, with a terminal group of spores.

Tilletia Tritici and *T. foetens* are the stink brands of wheat, so-called by reason of the strong smell of trimethylamine, or herring brine, given out by the brand spores. The species differ in the character of the epispore, which is smooth in *T. foetens*, reticulate in *T. Tritici*. In both cases brand spores are produced in the ovaries of the host, all tissues of which, except the outer coat, are destroyed. The spore masses, if garnered with the crop, damage

[1] Massee, I., 1914.
[2] Harper, 1899 i; Werth and Ludwig, 1912.   [3] Federley, 1904.

the grains with which they are threshed or ground. The infected flour and chaff or straw are a cause of disease in man and animals.

On the germination of the brand spore of *T. Tritici* the nucleus passes into the promycelium and divides three or more times. Eight basidiospores, or occasionally a larger number, are budded off in a bunch at the tip of the basidium (fig. 216 *a*), and each receives a single nucleus and is violently discharged[1]. Short conjugating tubes grow out and connect neighbouring spores, often before they are shed (fig. 216 *b*). After conjugation the spores may become septate and, from those which contain two nuclei, filaments of binucleate cells grow out, and may give rise to conidia which are also binucleate. It is the hyphae of binucleate cells which bring about infection, pushing between the

Fig. 216. *Tilletia Tritici* (Bjerk.) Wint.; *a*, basidium thirty hours after rupture of brand spore; *b*, conjugation of basidiospores; × 300; after Plowright.

cells of the host seedling. Nuclear fusion takes place in the young brand spores[2]. This is the usual life history, but there is evidence that in some specimens of *T. Tritici*, as of *Ustilago Tragopogi-pratensis*, nuclear fusion takes place soon after nuclear association[3], and the parasitic mycelium consists of cells with single, diploid nuclei.

In species of *Doassansia* (fig. 217 *a*), *Entyloma* (fig. 217 *b*) and *Urocystis* (fig. 218), a mycelium of binucleate cells has been observed in the tissues of the host[4], and nuclear fusion in the young brand spore; but *D. Sagittaria*[5] has a life history similar to that of *Ustilago Maydis*.

Tuburcinia primulicola[6] forms a mycelium of uninucleate cells in the tissues of species of *Primula* and gives rise to uninucleate conidia on the young flower. When the flower opens the conidia

[1] Buller and Vanterpool, 1925.　　[2] Rawitscher, 1914.　　[3] Dastur, 1921.
[4] Dangeard, 1894 i.　　[5] Rawitscher, 1922.　　[6] Wilson, 1915.

conjugate in pairs, and those containing two nuclei germinate to
form the sporophytic mycelium on which the brand spores are
borne. The arrangement here differs from the ordinary life history
of the smuts in the longer continuance and parasitic character of
the gametophyte and in that respect suggests a comparison with
the rusts.
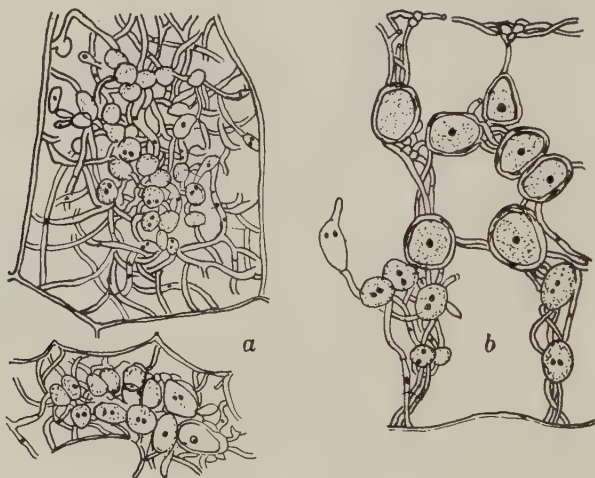
Fig. 217. Formation of brand spores; *a, Doassansia Alismatis* (Nees)
Corn.; *b, Entyloma Glaucii* Dang.; after Dangeard.

Fig. 218. *Urocystis Anemones* (Pers.) Wint.; mycelium and young spore
ball; after Lutman.

PROTOBASIDIOMYCETES

In the Protobasidiomycetes the nucleus of the basidium under-
goes two successive divisions and the daughter nuclei are separated
by walls cutting the basidium into four uninucleate cells. Each
of these gives rise to a single spore into which the nucleus passes.
The number of spores is thus definite and limited, and the basi-

dium is regularly septate. The direction of the septa may be transverse, longitudinal, or oblique.

The group includes between 1800 and 1900 species, most of which belong to the Uredinales. The members of this alliance differ from the other Protobasidiomycetes in being obligate parasites on green plants, with an endophytic mycelium and highly specialised spore forms. Many of them possess sexual organs, though the normal union of male and female nuclei has in every case been replaced by some form of apogamy. Development takes place within the tissues of the host, and the cuticle is not ruptured till the spores are ready for dispersal.

In the Auriculariales and Tremellales, on the other hand, the species are obligate saprophytes or facultative parasites, and form outside the substratum a large, gelatinous sporophore, on the surface of which the spores develop.

The distinctions between the three alliances may be summarised as follows:

Obligate parasites, developed within the tissues of
    the host; basidia transversely septate   UREDINALES

Saprophytes or hemi-saprophytes, forming a gela-
    tinous, exposed sporophore

Basidia transversely septate   AURICULARIALES
Basidia obliquely or longitudinally septate   TREMELLALES

UREDINALES

The rust fungi, members of the Uredinales[1], or Aecidiomycetes, including some 1700 species, are without exception obligate parasites on the stems, the sporophylls, and especially the leaves of vascular plants, usually on angiosperms or gymnosperms, but in one or two cases on ferns.

The mycelium ramifies between the cells of the host, sends haustoria[2] into the cells, and may induce hypertrophy with consequent curling and malformation of the infected part. The storage of starch may be stimulated; it is so abundant in the hypertrophies caused by the aecidial mycelium of *Puccinia Caricis* on *Urtica*

[1] Tulasne, 1854; de Bary, 1887; Plowright, 1889; Eriksson, 1894–1905; Sappin-Trouffy, 1896; Tranzschel, 1904; Maire, 1911; Ramsbottom, 1912; Grove, 1913 ii; Bailey, 1920.
[2] Nemec, 1911 ii.

parvifolia that these are used as food by the Himalayans; the products of one or two other species are similarly employed. Where
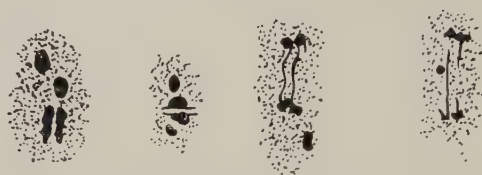
Fig. 219. *Uromyces Poae* Raben.; conjugate divisions in aecidium, × 1330; after Blackman and Fraser.

Fig. 220. *Gymnosporangium clavariaeforme* Rees; first division in basidium, × 1460; after Blackman.

the mycelium grows in the perennial tissues of the host, it is itself perennial.

The nuclear divisions of the rusts[1] have undergone considerable simplification; in the vegetative cells the chromatin appears to be drawn apart as undifferentiated masses (fig. 219) between which

[1] Poirault and Raciborski, 1895; Holden and Harper, 1903; Blackman, 1904; Blackman and Fraser, 1906 i; Arnaud, 1913; Moreau, Mme, 1914.

a kinoplasmic thread represents the spindle; when conjugate divi-
sion occurs the spindles of the members of the synkaryon lie
parallel one to another. The divisions of the fusion nucleus of
the teleutospore, however, still show some of the characters of a
meiotic phase. The chromatin displays a synaptic contraction, and
the spireme breaks up into segments (fig. 220) which, in favour-
able cases, appear to be double throughout their length. The spindle
is extra-nuclear, and lies free in the cytoplasm before coming into
contact with the chromatin. In many cases the chromosomes
apparently lose their individuality after passing on to the spindle,
and travel in irregular masses to the poles.

On the mycelium several kinds of spore are produced: minute
spermatia in spermogonia, aecidiospores in aecidia, uredospores
and teleutospores, sometimes mixed, sometimes separate, in more
or less definite sori. One or more spore forms may be lacking, but
teleutospores are almost always present, and on them the classifi-
cation of the alliance is based.

It was some time before spores of so many kinds were recognised
as belonging to the same fungus, and the old generic names of
stages other than the teleutospore, such as *Aecidium*, *Caeoma* and
Uredo, still survive as descriptive terms.

The **teleutospores** (figs. 221, 222) may be unicellular or made
up of two or more cells, forming a compound structure, each cell
of which develops independently. One-celled teleutospores oc-
curring exceptionally in two-celled species are known as **meso-
spores.**

The teleutospores may be massed together and encrusted in the
tissues of the host, undergoing further development *in situ* (fig.
223), or they may be readily detached and carried away by the
wind or other agencies. Development may continue as soon as
conditions are favourable, or only after a resting period, usually
in the spring following the formation of the teleutospores. In
either case the nucleus of the teleutospore cell ultimately under-
goes two successive divisions; the daughter nuclei are separated
by transverse walls, so that four uninucleate cells are formed.
This is the septate basidium. From each cell a pointed sterigma
arises, its end dilates, a basidiospore, or sporidium, is formed,
and the latter receives the nucleus and cytoplasm of the parent cell.

In *Coleosporium*, *Ochropsora* and *Chrysopsora* nuclear division
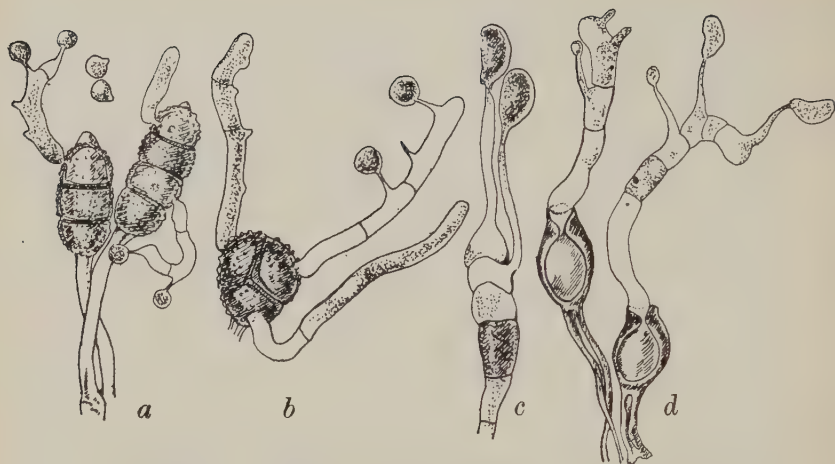
Fig. 221. Developing teleutospores; *a, Phragmidium bulbosum* Schm.; *b, Triphragmium Ulmariae* Lk.; *c, Coleosporium Sonchi* Lév.; *d, Uromyces appendiculatus (Fabae)* Lév.; after Tulasne.
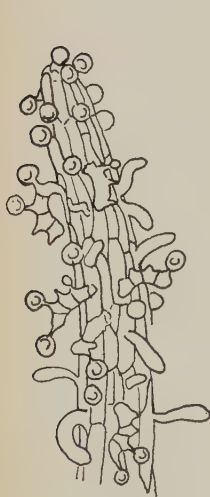
Fig. 222. *Cronartium asclepiadeum* Fr.; teleutospore mass with promycelia and spores; after Tulasne.

Fig. 223. *Melampsora betulina* Desmaz.; developing teleutospores; after Tulasne.

and septation take place within the wall of the single-celled teleuto-spore, and from it basidiospores are budded out, so that the teleutospore functions directly as a basidium; in other genera the teleutospore wall is thickened and does not readily admit of ex-pansion. Development then occurs after the extrusion of the contents of the teleutospore cell as a promycelium, delimited only

Fig. 224. *Gymnosporangium clavariaeforme* Rees; developing teleutospores; × 666.
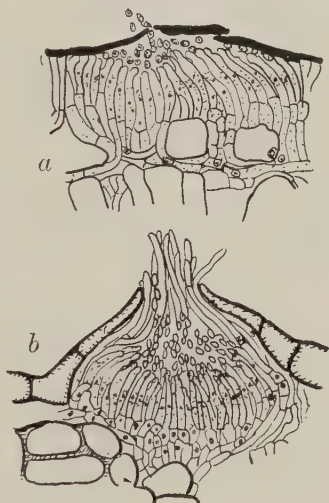
Fig. 225. *a, Phragmidium violaceum* Wint., × 330; *b, Gymnosporangium clavariaeforme* Rees, × 260; sper-mogonia; after Blackman.

by a delicate membrane (fig. 224). Nuclear and cell division take place in the promycelium, and from it the sterigmata arise.

When the basidiospores are ripe they are shot off successively with some violence, reaching a distance from the sterigma of 0·2 to 0·9 mm.[1] before they begin to fall downwards under the influence of gravity; just before ejection a drop of fluid appears at the base of the spore and is later carried away with it. Where the develop-ment of the teleutospore cell occurs *in situ*, the promycelium takes up a position which allows the basidiospores to be shot away from the sorus.

Should the basidiospore reach a suitable habitat, it germinates. Its germ tube penetrates the cuticle of the host and forms a

[1] Buller, 1924.

mycelium of uninucleate, or in some cases, of multinucleate[1] cells bearing spermogonia and aecidia.

The **spermogonium** is usually found on the adaxial side of the leaf; it consists of a group of parallel, simple or branched[2], outwardly directed spermatial hyphae, arising from a small-celled tangle below the cuticle or epidermis of the host. In most species the outer hyphae of the group form paraphyses, so that the spermogonium is restricted in extent and assumes a flask-shaped outline; the paraphyses push between the epidermal cells of the host and project from a narrow ostiole (fig. 225 b). In simpler forms, such as *Phragmidium*, the spermogonium is indefinite in extent (fig. 225 a).

The spermatial hypha is long and narrow, with an elongated nucleus; from its tip successive spermatia are cut off (fig. 226). When mature the spermatium is a small, more or less oval cell enclosed in a thin wall. The cytoplasm is finely granular, without

Fig. 226. *Gymnosporangium clavariae-forme* Rees; development of spermatia, × 1185; after Blackman.

reserve material, and the nucleus is of relatively large size. When cultivated in solution of cane sugar or honey, spermatia have been induced to undergo yeast-like budding, and this has also been observed under natural conditions; but, though many attempts have been made, it has so far proved impossible to bring about the formation of a mycelium. It seems clear, therefore, that spermatia are useless as agents of infection, and they differ also in structure from ordinary asexual spores. On the other hand, it was long ago suggested that they may be male reproductive elements; this is consistent with their large nuclei and lack of reserve material, and is not invalidated by the fact that they possess some slight power of germination; they are certainly not sperm cells, and may best be regarded as reduced antheridia, comparable to those of the Pyrenomycetes and the red algae. In any case they are now no longer functional. There is some evidence that they were formerly

[1] Lindfors, 1924.   [2] Fromme, 1912.

distributed by insects, since the latter appear to be attracted by the sticky masses which often accumulate outside spermogonia. The scent of *Puccinia suaveolens* and the yellow or orange patches about the aecidia and spermogonia of several species may have had a similar function.

The **aecidia** are cup-shaped structures (fig. 227) occurring in

Fig. 227. *Puccinia Graminis* Pers.; *a*, infected leaf of *Berberis vulgaris*, nat. size; *b*, group of aecidia, ╱ 5. *Uromyces Poae* Raben.; *c*, infected leaf of *Ranunculus Ficaria*, nat. size; *d*, group of aecidia, × 20; E. J. Welsford del.

groups, usually on the abaxial side of the leaf, and known as **cluster cups**; in them the **aecidiospores** are produced in basipetal rows (fig. 228), alternating with small, intercalary cells which sooner or later disintegrate. The mature aecidiospore is usually subglobose or polyhedral; it is enclosed in a thick wall provided with several germ pores, and contains red, yellow, or orange pigment, and always two nuclei. Under moist conditions it becomes turgid and rounded away from the neighbouring cells, its attachment to the intercalary cell immediately below it is weakened and at last overcome, and the spore is discharged with a force sufficient to carry it to a distance of from one to fifteen

millimetres[1] away from the leaf. It may be noted in this connection
that the aecidiospore is much larger and heavier than the basidio-
spore. Sometimes clumps of from sixty to a hundred and fifty
spores are shot away together. In germination a hypha is put out
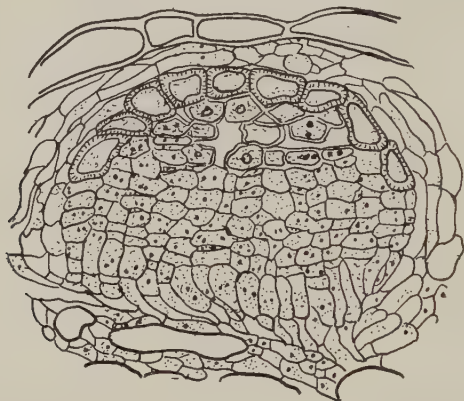
Fig. 228. *Uromyces Poae* Raben.; aecidium just before the epidermis is
broken through, × 310; after Blackman and Fraser.

which enters the host plant through a stoma, and penetrates into
the intercellular spaces.

At the periphery of the aecidium the aecidiospore mother cells,
instead of each dividing to form an aecidiospore and an intercalary
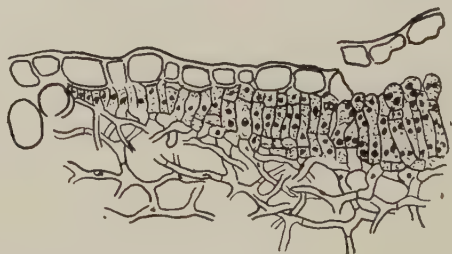
Fig. 229. *Phragmidium violaceum* Wint.; caeoma, × 240; after Blackman.

cell, acquire thick, striated walls, lose their contents, and form the
sides[2] of a sheath, or **pseudoperidium**, about the sporogenous part.
Centrally, where the pseudoperidium arches over the aecidial
contents, it is derived from the cells first cut off in each row.
When the uppermost functional spores are ripe the pseudoperi-

[1] Buller, 1924.   [2] Kursanov, 1914.

dium pushes through the epidermis of the host, is itself ruptured, and exposes the spores. It divides into teeth and becomes recurved, so that the characteristic cluster cup is produced. The pseudo-peridium is in some species elongated and either cylindrical or
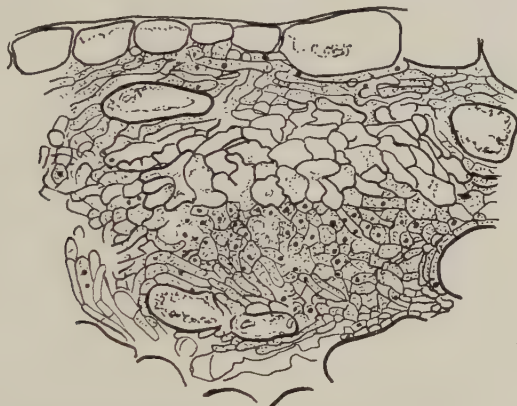
Fig. 230. *Uromyces Poae* Raben.; young aecidium, × 370; after Blackman and Fraser.
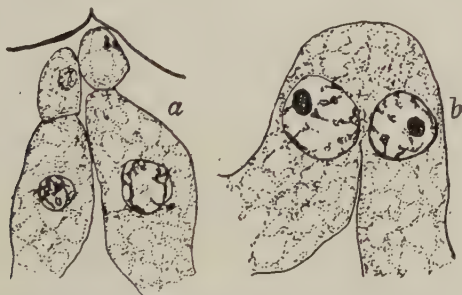
Fig. 231. *Phragmidium speciosum* Fr.; *a*, fertile and sterile cells; *b*, fusion of two fertile cells; after Christman.

inflated, giving the forms known as **roestelia** and **peridermium**, so-called from their old generic names. In others, such as the species of *Phragmidium* and *Melampsora*, the developing spores are sur-rounded only by a few sterile filaments. Such forms (fig. 229), to which the old generic name **caeoma** is applied, are probably primitive, and occur in the same species as spermogonia of indefinite extent.

The development of the aecidium[1] begins either directly below the epidermis or deeper in the tissues of the host by the massing of hyphae (fig. 230), which give rise to a more or less regular plate of cells. Each of these usually cuts off a terminal **sterile** cell
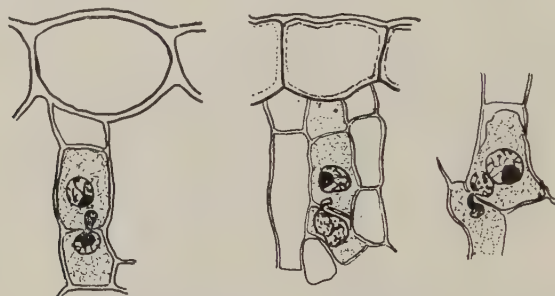
Fig. 232. *Phragmidium violaceum* Wint.; migration of second nucleus into fertile cell of caeoma, × 950; after Blackman.
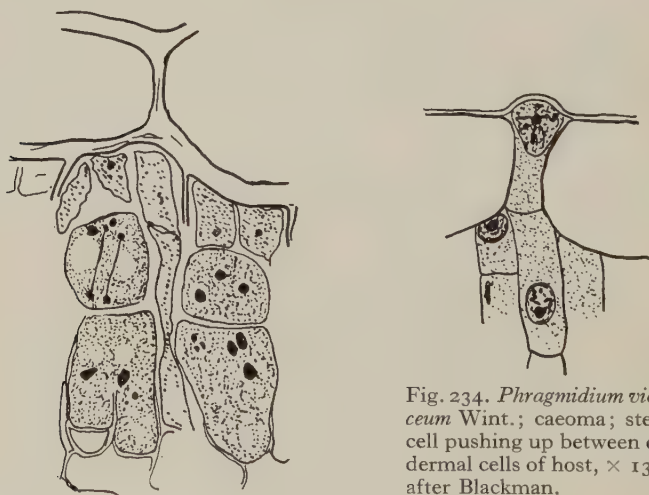
Fig. 233. *Melampsora Rostrupi* Wagn.; paired fertile cells, × 1200; after Blackman and Fraser.
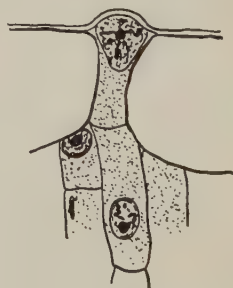
Fig. 234. *Phragmidium violaceum* Wint.; caeoma; sterile cell pushing up between epidermal cells of host, × 1300; after Blackman.

(figs. 231, 232, 233) which ultimately degenerates; it sometimes pushes up to the surface (fig. 234), and may possibly represent the remains of a trichogyne. Its larger sister cell is the oogonium,

[1] Blackman, 1904; Christman, 1905; Blackman and Fraser, 1906 i; Olive, 1908; Grove, 1913 ii; Fromme, 1912, 1914; Welsford, 1915; Thurston, 1923.

sometimes known as the **fertile** or **basal** cell, and contains cytoplasm and a single nucleus (fig. 231 a). As has already been seen, the spermatia are functionless, and normal fertilisation does not occur. The oogonia may unite laterally in pairs (fig. 231 b), so that compound, binucleate cells are formed; they may similarly pair with cells below them (fig. 235), or may each receive a second nucleus by migration (figs. 232, 236 a) from a vegetative cell. They proceed at once to cut off binucleate aecidiospore mother cells, each of which divides to separate an intercalary cell below from the larger aecidiospore above. Exceptionally, cells with two nuclei may be observed before the oogonia are differentiated, nuclear migration (fig. 237) taking place between cells at the base of the very young aecidium. In this case the oogonia are binucleate from their first formation.

Fig. 235. *Triphragmium Ulmariae* (Schum.) Link; primary uredosorus; condition intermediate between migration and conjugation of fertile cells; after Olive.
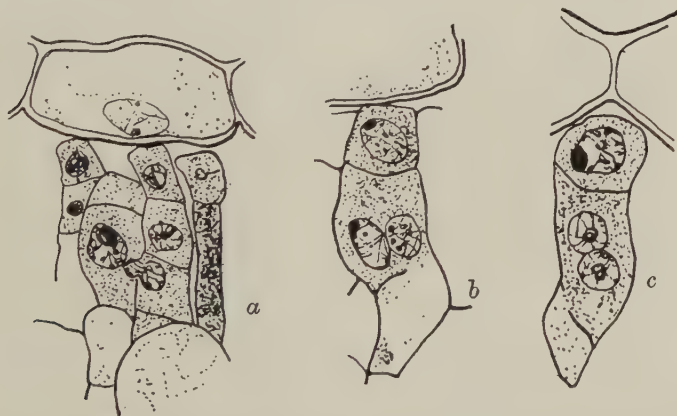
Fig. 236. *Phragmidium violaceum* Wint.; caeoma; a, migration of nucleus from vegetative cell of one hypha to fertile cell of another, $\diagup$ 1040; b and c, binucleate cells showing the pore through which the second nucleus has passed, $\times$ 1010; after Welsford.

Since the association of nuclei is sometimes brought about by the fusion in pairs of similar fertile cells, the suggestion has been

put forward[1] that these may be undifferentiated or slightly differentiated gametangia, and their union a normal conjugation. The migration of the nucleus from a vegetative to a fertile cell is assumed to be pathological, and the spermatia are looked upon as abortive conidia. The hypothesis is suggestive, but does not account for all the facts observed.

The aecidiospores, accordingly, may best be regarded as the products of a pseudapogamous process by means of which two nuclei

Fig. 237. *Uromyces Poae* Raben.; nuclear migrations in young aecidium, × 950; after Blackman and Fraser.

Fig. 238. *Puccinia Falcariae*; branched fertile cell of aecidium or primary uredosorus, × 1200; after Dittschlag.

become associated within a single cell. As in the smuts, they do not fuse at once, but divide simultaneously (fig. 233), constituting a synkaryon. The binucleate oogonium is the first stage of the diplophase and the aecidiospores serve as accessory spores of the sporophyte, corresponding, in this respect, to the carpospores of the red algae.

In most cases each oogonium, after the fertilisation stage, gives rise to a single chain of spores; but occasionally the oogonia branch[2], and thus produce two or more spore rows. In certain

[1] Christman, 1905; Olive, 1908.   [2] Christman, 1907; Dittschlag, 1910.

species branching is the normal condition, the oogonia regularly forming a number of buds (fig. 238), from each of which a single spore is produced. The spore mother cell divides in the usual way, separating the aecidiospore from its sister cell below, but the latter here forms an elongated stalk (fig. 239) instead of a narrow intercalary cell. The method of formation is closely similar to that of a uredospore, and the fructification is still known as a **primary uredosorus** in reference to its appearance relatively early in the year.

Fig. 239. *Phragmidium Potentillae-Canadensis* Diet.; *a*, conjugation; *b*, branched fertile cell; after Christman.

The mycelium formed by the aecidiospores consists of binucleate
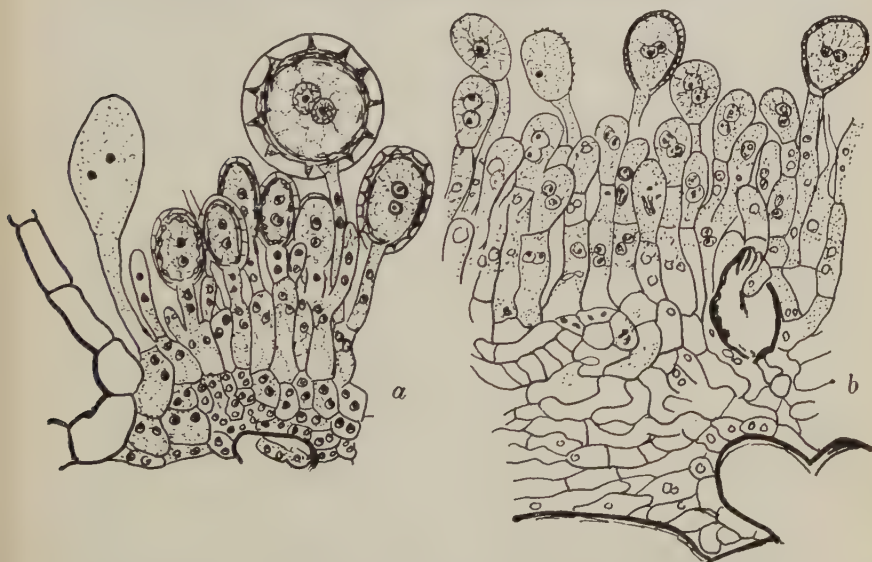
Fig. 240. *Phragmidium Rubi* Pers.; *a*, uredosorus, × 600; after Sappin-Trouffy; *Phragmidium violaceum* Wint.; *b*, uredosorus, × 480; after Blackman.

cells; it may bear uredospores or teleutospores. The **uredospores** are produced in groups, or **uredosori** (fig. 240), which may be

surrounded by paraphyses or by a pseudoperidium[1] similar to that found in aecidia. In the young sorus a regular layer of fertile or basal cells is formed, and from these the uredospore mother cells arise. In a few species they appear in vertical rows like aecidiospore mother cells, and divide to form uredospores and small intercalary cells (fig. 241), but in most cases they grow out as buds from the basal cell, and give rise to a uredospore and stalk (fig. 240). The stalk remains narrow while the uredospore enlarges, its contents acquire an orange or yellow colour and its wall is thickened and roughened by minute projections. Two or more germ pores are usually present, and the uredospore, like the cells from which it is developed, is invariably binucleate. It gives rise on germination to a mycelium of binucleate cells, on which teleutospores or further crops of uredospores are formed, and thus serves as an accessory spore of the sporophyte.

Fig. 241. *Coleosporium Sonchi*; uredosorus, × 545; after Holden and Harper.

Rusts occurring under very dry conditions may produce a type of uredospore with specially thickened walls. These are known as **amphispores**.

Sooner or later the mycelium of binucleate cells gives rise to teleutospores, which are commonly grouped in **teleutosori** (fig. 242). Like the uredospores they may be associated with paraphyses, and, like them, they arise as branches from basal cells. The branch usually divides to cut off a stalk cell below, and the simple or compound teleutospore (fig. 243) may be derived from the terminal cell, or the latter may function as a buffer[2] and the teleutospore be formed from the penultimate cell. Like the segments of the mycelium on which it is borne, the teleutospore cell is binucleate (fig. 244). When the wall is fully thickened the two nuclei fuse, and the cell passes into a resting state. On the renewal of its development two nuclear divisions occur, the basidiospores are formed and the haploid phase initiated. In *Puccinia Arenariae*[3], however, the basidium, after the first mitosis, divides into two uninucleate cells; each nucleus divides again and each cell gives

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[1] Moss, 1926.   [2] Dodge, 1918 i, ii.   [3] Lindfors, 1924.

rise to one binucleate spore, so that the synkaryon begins in the basidiospore.

A striking similarity exists in the arrangement of the three kinds
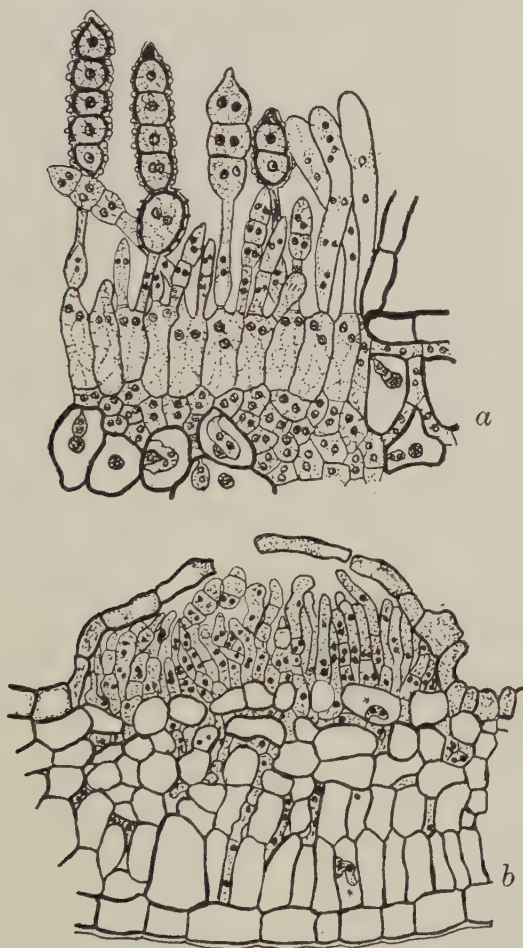
Fig. 242. *Phragmidium Rubi* Pers.; *a*, teleutosorus, × 240; after Sappin-Trouffy; *Phragmidium violaceum* Wint.; *b*, young teleutosorus, × 240; after Blackman.

of sporogenous cells. The uredo- and teleutosori are clearly comparable; both are of indefinite extent, with or without a border of paraphyses, and both consist of plates of basal cells from which the spore mother cells arise as branches, dividing to produce the

simple or compound spore and the stalk cell. Sometimes, however, the uredospores are borne in rows, one below the other, and the sister cell of the spore forms a narrow intercalary cell instead of a stalk. This arrangement, and that of the so-called primary uredosorus, link the true uredosorus with the aecidium, indicating the homology of the stalk and intercalary cells and suggesting a comparison between the binucleate oogonium and the basal cell of the uredosorus. In the simplest aecidia, those of the caeoma type, the group of oogonia is of indefinite extent. The aecidium, in fact, is no more a definite organ than the uredo- or teleutosorus, and appears so in the more advanced forms only because of the modification of its peripheral cells to form a pseudoperidium. The essential distinction lies, not in the morphology of the sorus, but in the association of two nuclei which takes place in the aecidium. In its general structure the spermogonium, consisting, as it does, of a series of spermatial hyphae, with or without circumjacent paraphyses, is not very different from the other sori, and, in its simplest form, is also of indefinite extent.

In many rusts one or more spore forms are omitted; the case in which a primary uredosorus is substituted for the typical aecidium has already been described. Such species, and those in which the aecidium alone is lacking, are distinguished by the prefix **brachy-**.

Hemi- indicates the presence of uredo- and teleutospores without aecidia or spermogonia.

The suffix **-opsis** is used for species with aecidia and teleutosori; they lack uredosori, but a few uredospores are sometimes found in the teleutosorus.

Micro- and **lepto-** forms have teleutospores with a few uredospores and sometimes spermogonia. The teleutospores germinate in the former type only after a period of rest, in the latter as soon as they reach maturity.

Species with the full complement of spores are distinguished by the prefix **eu-**.

In -opsis forms and in brachy- forms with primary uredosori the alternation of generations is the same as in eu- species, for the peculiarity of the second is that the aecidiospores are produced on stalks instead of in chains, while in the first only the uredospores, the accessory spores of the sporophyte, are lacking. In

Fig. 243. *Puccinia Podophylli* S.; fertile cell of teleutosorus giving rise to teleutospores; after Christman.
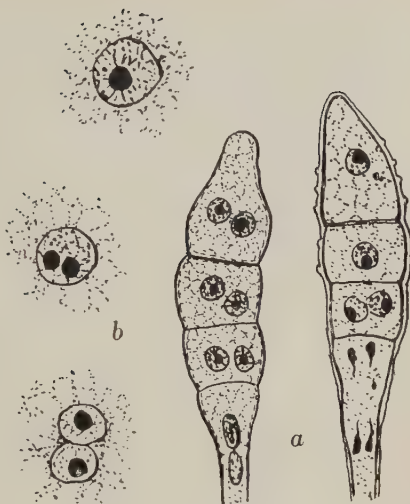
Fig. 244. *Phragmidium violaceum* Wint.; *a*, teleutospores, × 1080; *b*, fusion of nuclei in teleutospore cell, × 1520; after Blackman.

Fig. 245. *Puccinia Malvacearum* Mont.; *a*, conjugation of unequal cells at base of teleutosorus; *b*, teleutospore; both after Werth and Ludwig. *Puccinia Podophylli* S.; *c*, migrations at base of teleutosorus; after Christman.
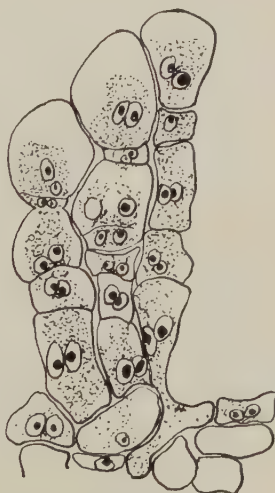
Fig. 246. *Endophyllum Sempervivi* Lév.; fertile cells and spores; after Hoffmann.

micro- and lepto- species the basidiospore germinates to produce, as in eu- forms, a mycelium of uninucleate cells on which spermogonia are sometimes borne. The cells become binucleate either during vegetative development or at the base of the young teleutosorus (fig. 245), and binucleate teleutospore cells, in which nuclear fusion occurs, are produced in the usual way. As in species with aecidia, the binucleate condition may arise either by the fusion in pairs of uninucleate cells, or by the migration of a nucleus from one uninucleate cell to another. The sporophyte may thus include
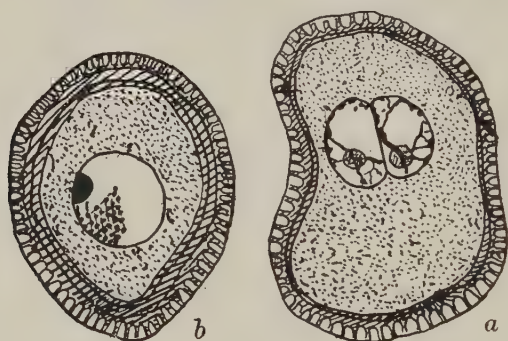
Fig. 247. *Endophyllum Sempervivi* Lév.; *a*, nuclear fusion in spore; *b*, synapsis in fusion nucleus; after Hoffmann.

an abbreviated vegetative mycelium, or may be limited to the basal cell of the teleutosorus and its products.

A diplophase of still briefer duration[1] is found in *Endophyllum* and *Kunkelia*. In both genera binucleate aecidiospores (fig. 246) are formed in the usual way, but their nuclei fuse (fig. 247) as soon as maturity is reached, and the aecidiospore develops like a teleutospore cell, with the protrusion of its contents as a promycelium, and the formation (fig. 248) of four basidiospores. A clue to the origin of this condition may possibly be found in *Kunkelia nitens*[2], the caeomata of which are morphologically indistinguishable from those of *Gymnoconia interstitialis*, a form with a normal life cycle. The two species differ markedly in their distribution, *Gymnoconia* occurring in America to the north and east of *Kunkelia*, with only slight overlap. It has been suggested that the warmer climate in which *Kunkelia* flourishes renders the thick-walled teleutospore

[1] Barclay, 1891; Hoffmann, 1912.   [2] Kunkel, 1914; Moreau, 1920.

unnecessary[1]. Basidiospore formation without fusion or meiosis has been recorded for *K. nitens*[2].

Euapogamous development takes place in *Endophyllum Euphorbiae*[3] on *Euphorbia sylvatica*; the oogonia and aecidiospores are uninucleate throughout their development, the aecidiospore forms a promycelium of three or four cells, and neither nuclear association nor nuclear fusion is found at any stage, the
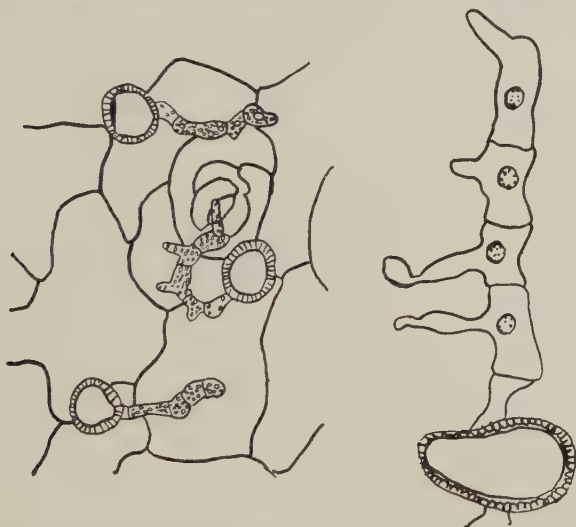
Fig. 248. *Endophyllum Sempervivi* Lév.; spores giving rise to promycelium; both after Hoffmann.

diplophase being wholly omitted. Uninucleate aecidiospores likewise occur in *Aecidium leucospermum*[4].

In many rusts the gametophytic and sporophytic mycelia develop on different hosts. It is not surprising that the spore forms of such **heteroecious** species were recognised and described some time before they were identified as stages in the life of a single fungus. The final proof of the relationship of the aecidia and spermogonia on the one hand, and the uredo- and teleutosori on the other, was given by de Bary in 1865 for the wheat rust, *Puccinia Graminis*. In this plant the haploid mycelium occurs on the leaves of the barberry, *Berberis vulgaris*, and the diploid growth on wheat, rye, oats, and other grasses.

[1] Arthur, 1917; Olive and Whetzel, 1917; Dodge, 1923.
[2] Dodge and Gaiser, 1926.   [3] Moreau, 1920.   [4] Kursanov, 1917.

Long before this relationship was demonstrated, and even before the fungal origin of the disease was known, farmers had begun to suspect some harmful connection between barberry bushes and the crop, and had observed that dark areas of blackened and injured wheat were apt to occur in the neighbourhood of such plants. In the State of Massachusetts an Act was passed requiring the extirpation of all barberries before a given date in 1760, and writers of the period called attention to the belief among husbandmen that the barberry had "a mysterious power" of blighting the wheat which grew near it. It was not till 1797 that the wheat disease was identified as a fungus, and the first artificial infections were made in 1816.

It seems unlikely that the heteroecious condition is primitive[1], and it has been suggested that it arose in relation to hosts with a short vegetative period. There would be then hardly time for the production of the full complement of spores, and the fungus might either shorten its life history, continuing in the autoecious condition as a micro- or other abbreviated form, or some of the spores might become adapted to life on a new host. Aecidiospores are produced relatively early in the season, they fall on hundreds of leaves besides those of their host, and the germ tubes in their case enter through stomata. If then an aecidiospore germinated and penetrated a satisfactory new host, a mycelium might develop, and further adaptations might fix the heteroecious habit. Gramineae and other hosts with refractory cuticles are easily infected by germ tubes from the aecidiospores or uredospores which enter through the stomata, but not by those of the basidiospores which usually penetrate the walls of the epidermal cells. This fact may be significant in relation to the return of the rust to its gametophytic host each spring.

The Uredinales are divided into four families distinguished as follows:

Basidiospores borne on a promycelium extruded from the teleutospore cell	
Teleutospores stalked	PUCCINIACEAE
Teleutospores sessile	
Teleutospores arranged in series but separating later	CRONARTIACEAE
Teleutospores united in a flat layer under the epidermis	MELAMPSORACEAE
Basidiospores budded out from the teleutospore cell without a promycelium	COLEOSPORIACEAE

[1] Tranzschel, 1904; Olive, 1911; Grove, 1913 i.

PUCCINIACEAE

The teleutospores of the Pucciniaceae are provided with a stalk which is often well developed, but is in some cases short, or becomes detached at an early age. The teleutospores are one-celled in *Uromyces* (fig. 221 *d*) and *Hemileia*, two-celled in *Puccinia* and *Gymnosporangium* (fig. 224); they are made up of three cells in *Triphragmium* (fig. 221 *b*), and in *Phragmidium* (fig. 221 *a*) of three or more cells. *Gymnosporangium* is further characterised by the long pedicels of its teleutospores and by the fact that they are embedded in a gelatinous mass; the uredospores are solitary. The aecidiospores of *Phragmidium* and *Triphragmium* are produced in caeomata, in other genera they are formed in aecidia, with pseudoperidia, which, in *Gymnosporangium*, are commonly elongated to form flask-shaped or cylindrical roestelia.

The family includes some of the most highly developed of the Uredinales, but it includes also genera with caeomata. It may perhaps be linked with the Coleosporiaceae through *Zaghouania*, where the development of the teleutospore is of an intermediate type.

CRONARTIACEAE

In the Cronartiaceae the teleutospores are unicellular and sessile, but so closely packed that they simulate multicellular spores. In *Chrysomyxa* they form wavy crusts, and in *Cronartium*[1] (fig. 222) a cylindrical body. A pseudoperidium is present around the aecidiospores. The genus *Endophyllum* is sometimes placed here, sometimes a separate family is created for it. It differs from the rest of the Cronartiaceae and from most of the rusts in the fact that its basidia originate as aecidiospores. This character is probably reduced rather than primitive.

MELAMPSORACEAE

The teleutospores of the Melampsoraceae are sessile, loose in the tissue of the host in *Uredinopsis*, a genus infecting ferns, in other members of the family grouped in a flat layer under the epidermis. In *Melampsora* and its immediate allies they are uni-

[1] Colley, 1918.

cellular, in *Calyptospora* and *Pucciniastrum* they are divided by longitudinal walls into two or four cells.

The aecidiospores may be surrounded by a pseudoperidium or developed in a caeoma; in some cases a pseudoperidium is present around the uredosorus also.

<div align="center">COLEOSPORIACEAE</div>

The outstanding character of the Coleosporiaceae is the method of development of the unicellular teleutospore, the contents of which undergo septation directly (fig. 221 *c*), and, in *Coleosporium* and *Ochropsora*, without protrusion as a promycelium; in *Zaghouania*[1] the contents of the teleutospore divide within the teleutospore wall to form four cells, but emerge before the basidiospores appear.

The aecidia are cup-shaped in *Ochropsora*, but in *Coleosporium* and *Zaghouania* they are of the peridermium type with a cylindrical, more or less inflated pseudoperidium. This elaborate form of sorus makes it impossible to regard the Coleosporiaceae as primitive, though they may perhaps have branched off early from the line leading to the commoner rusts.

<div align="center">AURICULARIALES</div>

The Auriculariales are an assemblage of some fifty species occurring as saprophytes or hemi-saprophytes on wood, especially in the tropics, where a considerable number probably still await discovery. They resemble the Uredinales in their transversely septate basidia (fig. 249), but differ from them in their saprophytic habit and in the formation of a gelatinous fruit body on the surface of which the spores are borne. In many cases conidia as well as basidiospores are produced, and in some the basidiospores germinate to give rise to conidia, either directly or from the cells of a septate germ tube. There is no trace of a sexual apparatus, or any evidence that a sexual process once occurred except the fusion of two nuclei in the young basidium. In *Hirneola*[2] the mycelium shows numerous clamp connections which are especially frequent towards the sterile surface of the sporophore, but the nuclei are small and the details of their behaviour have not so far been elucidated.

In most of the Auriculariales the hymenium is fully exposed

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[1] Dumée and Maire, 1902.   [2] Green, 1925.

during development, but, in the genus *Pilacre*, a more or less definite peridium covers the young fructification and withers away as maturity is reached. This genus and the closely related *Pilacrella* are accordingly placed in a separate family, the Pilacreaceae, while the remaining genera form the Auriculariaceae.

The best known of the Auriculariaceae in Great Britain is *Hirneola Auricula-Judae*, the Jew's ear, which appears in winter

Fig. 249. *Auricularia sambucina* Mart.; *a*, transversely septate basidium with four sterigmata, × 300; *b*, a single, long sterigma with basidiospore attached, × 420; after Brefeld[1].

Fig. 250. *Exidia recisa* Fr.; group of longitudinally septate basidia; after Tulasne[2].

on the branches of the elder, forming brown, gelatinous sporophores with a resemblance to a human ear.

TREMELLALES

The Tremellales[3] include about one hundred species; their distribution is world wide, but they are massed chiefly in the tropics. Like the Auriculariales they are mainly saprophytes with for the most part a gelatinous sporophore of indefinite outline such as occurs in *Tremella*; in *Tremellodon* a stipitate fructification is produced with basidia on downwardly directed teeth which resemble those of the Hydnaceae.

[1] Brefeld, 1884.   [2] Tulasne, 1853.   [3] Burt, 1901; Wager, 1914 ii.

In the genus *Sirobasidium* the basidia are obliquely septate and arranged in chains, in other members of the alliance they are borne singly and are divided by two longitudinal septa formed successively and at right angles one to another (fig. 250). In *Hyaloria*, as in *Pilacre* among the Auriculariales, the hymenium is protected by a sheath of sterile hyphae.

As in the Auriculariales, no trace of a sexual apparatus has been found and the nuclei have so far proved too small for detailed study.

The South American genera, *Sirobasidium* and *Hyaloria*, are usually separated as distinct families, the Sirobasidiaceae and Hyaloriaceae; all other members of the alliance are included in the single family Tremellaceae.

AUTOBASIDIOMYCETES

The Autobasidiomycetes include between 11,000 and 12,000 species; they are cosmopolitan in distribution, often with large and conspicuous fructifications; their basidia never become septate. Though the sporophores show an immense variety of form, the essential facts of the life history are similar throughout the group; there is no trace of a sexual apparatus, but the young basidium contains two nuclei (fig. 251), and is commonly borne on a mycelium of binucleate cells[1], which may arise, as already described, by the association of two primary mycelia. The nuclei of the basidium fuse; the fusion nucleus undergoes two successive divisions, and, at the end of the second, the centrosomes attach themselves to the wall at points which become the positions of origin of the sterigmata[2]. The centrosome is carried up with the growth of the sterigma, and so enters the young spore; in the *Boleti*[3] it remains during this process connected with its nucleus by means of a cytoplasmic strand; in other cases the nuclei, after the second division, move into the lower part of the basidium (fig. 252); as they pass upwards again, stainable threads originating from the centrosomes, and perhaps analogous to astral rays, re-establish connection with them[4]; it is along these strands that the

[1] Cf. p. 246.
[2] Maire, 1902; Fries, 1911; Levine, 1913.
[3] Levine, 1913.   [4] Maire, 1902.

nuclei are drawn into the spores, being much elongated and com-
pressed as they pass through the narrow sterigmata. While spore
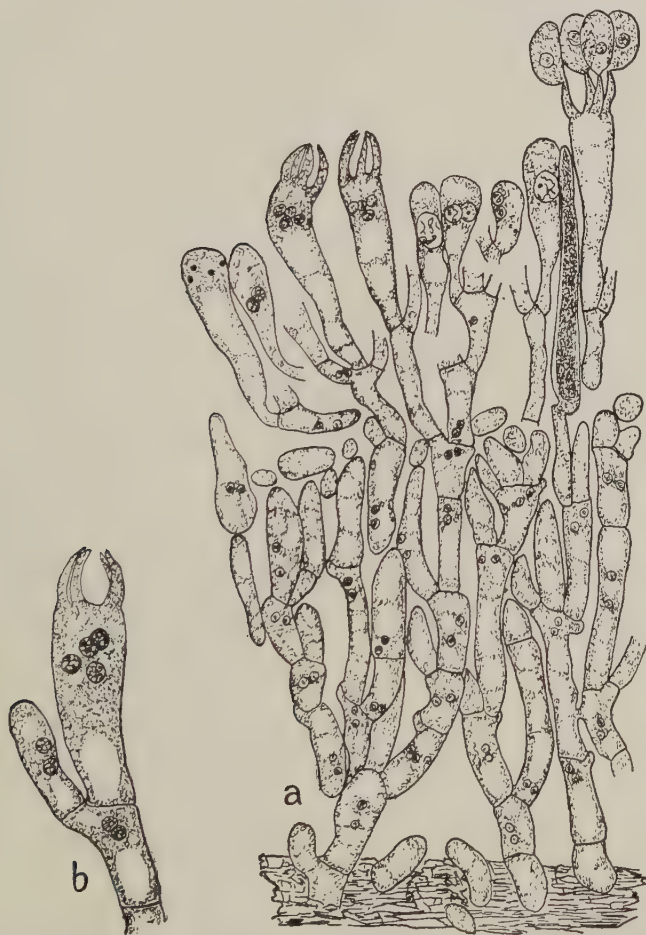
Fig. 251. *Hypochnus subtilis* Schroet.; *a*, hymenium of binucleate cells bearing
basidia; *b*, a young, binucleate basidium, and an older one in which the fusion
nucleus has divided to form the four spore nuclei and the sterigmata are
growing out; after Harper.

formation is in progress a vacuole forms in the basidium (fig. 253);
it is possibly the pressure due to the enlargement of this vacuole
that causes the flow of nuclei and cytoplasm into the spores.

The number of spores is almost invariably four, but there is one spore in *Pistillaria maculaecola*, two in the cultivated mushroom, in the genera *Calocera* and *Dacryomyces*, in *Coprinus bisporus*[1] and in some other species, three in *Coprinus narcoticus*, five in *Cantharellus Friesii*, six in species of *Cantharellus*, *Hypochnus* and *Exobasidium*, and eight in several of the Thelephoraceae, where, also, basidia with seven spores sometimes occur. The ripe spore is aseptate, though septa may be formed, as in *Dacryomyces*, before a germ tube is produced. In many species the spores are coloured,

Fig. 252. *Panaeolus campanulatus* (L.) Quél.; longitudinal section through part of a young gill, showing young, binucleate basidia, basidia after the nuclei have fused, and basidia with sterigmata and four nuclei; the numbers indicate successive stages in development; somewhat diagrammatic, × 1000.

and the epispore in some is sculptured. Conidia as well as basidiospores may be present, and chlamydospores are sometimes formed.

The hymenium, or fertile layer, includes basidia of all ages, from small, binucleate cells, the growth of which has only just begun, to mature, club-shaped specimens with sterigmata and spores projecting above the level of the hymenium, and older individuals from which the spores have been shed and which are in process of collapse. A young hymenium usually shows a preponderance of

[1] Lewis, 1906; Buller, 1922 ii.

uninucleate basidia (fig. 252), indicating that this stage endures for some time. In *Coprinus*[1] the mature basidia may be of two (fig. 254), three, or even four lengths, thus allowing a very large number simultaneously to reach maturity in a limited space; this arrangement is doubtless correlated with the successive development in that genus of basidia in different regions of the gill. The spores on the basidia are always symmetrically arranged, so as to be as far distant one from another as possible.

In addition to the basidia, the hymenium includes paraphyses, which have sometimes the appearance of young basidia, but are permanently sterile; they give support to the basidia, possibly supply them with water, and, since they have a much wider range of size than the basidia, provide an element of elasticity in the hymenium; moreover, in species where the cells of the hymenium are crowded, they prevent the too close contact of the basidia and obviate the overlapping of the spores.

In many species larger structures, known as **cystidia**[2] (figs. 254, 258), are also found in the

Fig. 253. *Stropharia semiglobata* Quél.; basidium during the formation of the spores, only three of the four spores are shown; × 1000.

hymenium; they may be cylindrical, club-shaped, or in the form of blunt or pointed hairs; in some species they produce characteristic secretions; in others, where they project considerably from the hymenium, they serve to keep adjacent hymenia apart.

All these elements are the terminal cells of richly branched hyphae which ramify in and form part of the tissue of the sporophore; their arrangement becomes more compact as they approach the hymenium, and thus the subhymenial layer is formed. Where the hymenium is spread over definite teeth or gills, or lines definite pores or chambers, as in the Hydnaceae, the Agaricaceae, the Polyporaceae, and many of the Gasteromycetales, the central tissue of the gill or tooth, or limiting tissue of the pore or chamber, is known as the **trama**, and consists of parallel or interwoven hyphae, sending out lateral branches to form the subhymenial layer and the hymenium. In *Psalliota campestris*[3] and other species the pileus and stem are composed of multinucleate cells, binucleate cells

[1] Buller, 1924.   [2] Knoll, 1912; Buller, 1924.   [3] Hirmer, 1920.

appearing first in the lamellae; in *Boletus granulatus*[1] the cells of the stipe are multinucleate, whereas those of the pileus and ring, as well as of the trama and its products, contain two nuclei; in most of the Autobasidiomycetes investigated, the binucleate condition supervenes early, before the primordium of the fructification is laid down. There is evidence that in nature the sporophores of species of *Coprinus* and *Panaeolus* are commonly derived from the
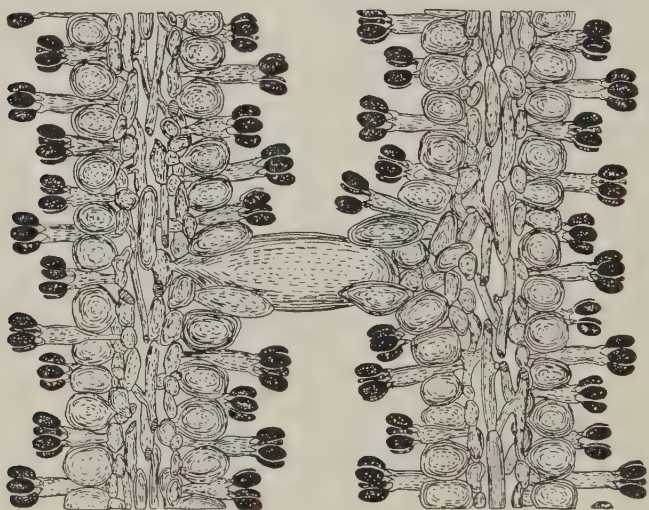
Fig. 254. *Coprinus lagopus*; transverse section through two gills of an unexpanded fruit body, showing long and short basidia, paraphyses, and a large cystidium, × 232; after Buller[2].

product of a single spore[3], or, in the case of heterothallic forms, of two. In other species it is possible that several mycelia may contribute to the formation of a single sporophore, which is not then an individual in the usual sense. It is worth noting that the sporophore of the Autobasidiomycetes differs from that of the Ascomycetes, in that the fertile hyphae of the latter are typically sporophytic, and the vegetative hyphae part of the gametophyte, whereas the whole tissue of the basidiomycetous fructification is normally of the same generation.

The efficiency of the apparatus may be gauged by the extraordinary quantity of spores set free. In round numbers a single

[1] Levine, 1913.   [2] Buller, 1924.   [3] Brefeld, 1877 i; Newton, 1926.

fructification of *Lycoperdon Bovista*, the giant puffball, produces 7,000,000,000,000, that of *Fomes applanatus*, which continues to liberate 30,000,000,000 a day for six months, 5,500,000,000,000, that of the mushroom, with a productive period of six days, 16,000,000,000, and that of *Coprinus sterquilinus*, which sheds spores during only eight hours, as many as 100,000,000[1]. Nevertheless the number of fungi of any given species remains approximately constant, which means, not merely that only one spore
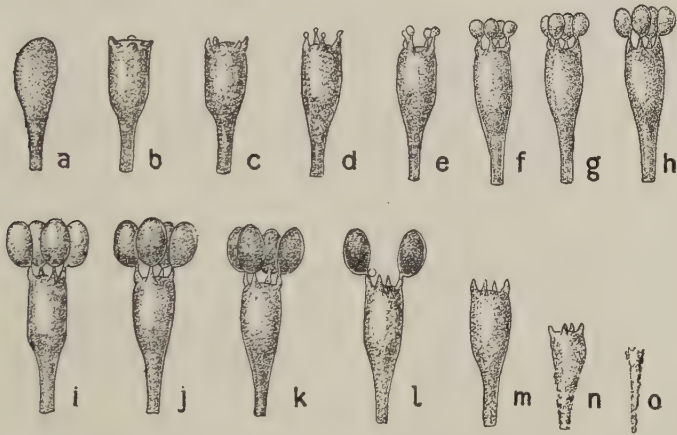
Fig. 255. *Coprinus sterquilinus*; stages in the development of a basidium; *a*, at 8 p.m., *b*, at 9 p.m., *c*, at 10 p.m., *d*, at 11 p.m., *e*, at midnight, *f*, at 2 a.m., *g*, at 2.30 a.m., *h*, at 3 a.m., *i*, at 8–11 a.m., *j*, at 7 p.m., *k*, midnight to 6 a.m., *l*, at about 6 a.m., *m*, at 6.10 a.m., *n*, at about 6.40 a.m., *o*, at about 7 a.m., × 272; after Buller[2].

from each sporophore is on the average successful in establishing itself and giving rise to a new specimen which reaches reproductive maturity, but that, where the mycelium gives rise to several fructifications, only one among all the spores from all the sporophores derived from the same plant attains success. The fact that many mycelia are perennial, and, as in the case of the hyphae of fairy rings, may endure even for hundreds of years, indicates a still smaller proportion of successful spores. It must be borne in mind, however, in this connection, that a sporophore, if derived from several mycelia, may represent the effective development of more than one spore, and, further, that in species where several strains

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[1] Buller, 1922 ii.   [2] Buller, 1924.

exist, a considerable surplus of spores may be needed to ensure the association of appropriate strains. With such vast numbers of spores available, it is not surprising that, under favourable conditions, large numbers of saprophytes, or epidemics of parasites, sometimes occur.

The Autobasidiomycetes include two alliances which may be distinguished as follows:

Hymenium exposed at maturity, and often
throughout development   HYMENOMYCETALES
Hymenium enclosed until after the spores are ripe   GASTEROMYCETALES

HYMENOMYCETALES

The Hymenomycetales constitute by far the largest subdivision of the Basidiomycetes, and include between 10,000 and 11,000 species, which may be para-sites or saprophytes. Interest centres around the evolution of the sporophore, which, in the simpler species, is a thin, smooth layer, spread over the surface of twigs or branches, with the hymenium fully exposed; effective protection of the basidia is attained on the gills of toadstools and in the pores of bracket-fungi.
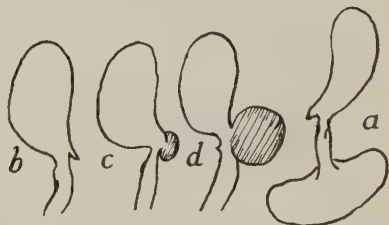
Fig. 256. *Sporobolomyces*; *a*, single cell budding; *b*, *c*, *d*, stages in the detachment of the bud, somewhat diagrammatic; after Kluyver and van Niel.

Associated with this development is the efficient dispersal of the spores by wind, the orientation in response to light and gravity of the stalked or laterally attached sporophore, and the method of ejection of the spore. The first indication[1] that a spore is about to be discharged is the appearance at its base of a drop of fluid (fig. 255 *l*); the drop grows till it reaches about one-quarter of the diameter of the spore, and is carried with it when the latter is shot off; the whole process takes a few seconds. A minute or two after the ejection of the first spore from a basidium a drop of fluid appears at the base of a second spore, and so on till all four are discharged and the collapse of the basidium takes place. An exactly similar method of discharge has been recorded in *Sporobolomyces*[2], a

[1] Buller, 1922 ii.   [2] Kluyver and van Niel, 1924.

unicellular fungus which multiplies by budding. The bud, or spore, is borne on a long sterigma (fig. 256), at the base of which a drop of water appears; it is violently discharged at maturity. This curious genus may well be the reduced offspring of an ancestor of the Hymenomycetales, bearing perhaps the same relation to
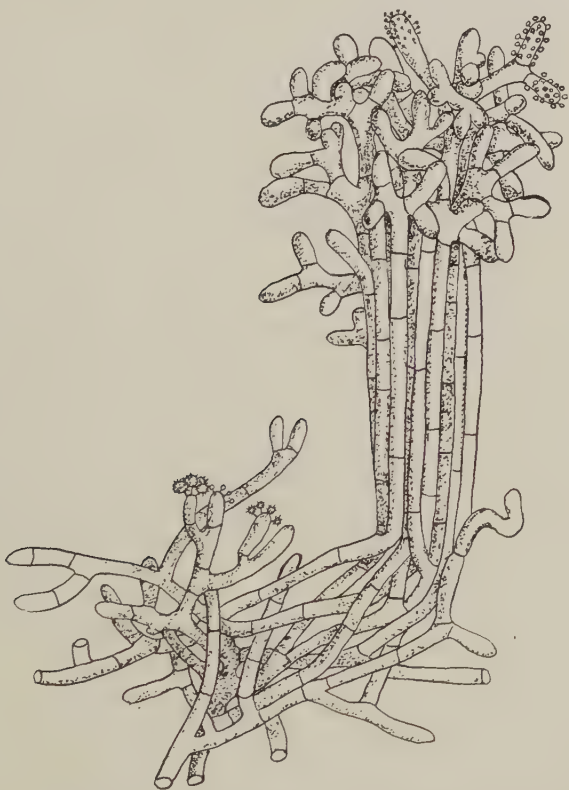
Fig. 257. *Tomentella flava* Bref.; group of small basidia and longer hyphae bearing conidia, × 202; after Brefeld.

the Thelephoraceae as the yeasts to the higher Plectascales, or its basidiomycetous method of spore dispersal may indicate a response to the same need, rather than a relationship.

On the ejection of the basidiospore, the latter, if borne on a pendulous gill or similar outgrowth of the sporophore, is shot horizontally forward to a distance of about 0·1 mm., which brings it to the middle

of the space between the gills or of the lumen of the pore; here, the momentum being exhausted, it executes a sharp turn through a right angle and falls vertically downwards under the influence of gravity. The fall is rapid at first, but, as soon as the spore leaves the shelter of the sporophore, it dries very quickly and, in dry air, the rate of fall is exceedingly slow, between 5 and o·5 mm. a second[1], according to the dimensions of the spore. In other words the rate of fall of thistledown is from thirty to three hundred times as rapid as that of a basidiospore.

A few of the Hymenomycetales, including members of the parasitic genus *Nyctalis*, multiply by means of chlamydospores as well as by basidiospores, and in *Dacryomyces*, *Tomentella* (fig. 257) and several others conidia are produced.

The alliance may be subdivided as follows:

Hymenium unilateral, spread over a smooth or corrugated surface	THELEPHORACEAE
Hymenium covering on all sides the smooth surface of branched or simple clubs	CLAVARIACEAE
Hymenium spread over spines	HYDNACEAE
Hymenium spread over gills	AGARICACEAE
Hymenium lining pores	POLYPORACEAE

THELEPHORACEAE

The Thelephoraceae include the simplest and probably the most primitive of the Autobasidiomycetes; among these are the species of *Hypochnus*[2], in which the cobwebby mycelium spreads over rotten branches, moss or grass, and gives rise to groups of basidia (fig. 251) and to numerous accessory spores; the hyphae show well-marked clamp connections, and binucleate cells. In the closely related *Tomentella* the basidiospores and conidia are brown or violet, and their epispores spiny; in *Aureobasidium* and *Pachysterigma* the basidia bear irregular numbers of spores. It was such facts which gave colour to the suggestion of a homology between the basidiospores and conidia.

In the large genus *Corticium* the sporophore is more compact and solid; it is smoothly spread over the substratum and is in some cases well described as resembling a splash of whitewash. The hymenium is thus fully exposed, facing outwards and unprotected against weather or marauding animals. Such a position is described as **resupinate**. *C. salmonicolor* is responsible for pink

[1] Buller, 1922 ii.   [2] Harper, 1902; Kniep, 1915, 1917.

disease[1], a serious affection on rubber, tea, and other crops. The closely related genera *Peniophora* and *Hymenochaete* differ from *Corticium* mainly in the presence of cystidia, which are brown and thick-walled in *Hymenochaete* (fig. 258), while in *Peniophora* the walls are thin and the tips encrusted with particles of lime; both

Fig. 258. *Hymenochaete Cacao* Berk.; basidia and cystidia; after Hennings[2].
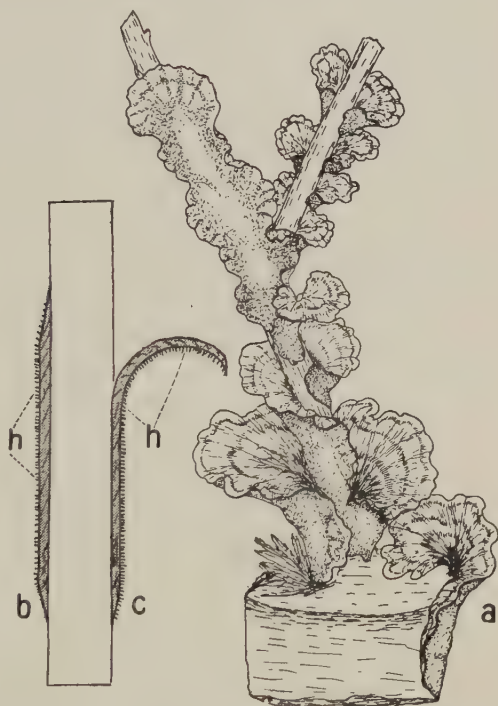
Fig. 259. *a*, *Thelephora tabacina* (Sow.) Lév.; resupinate sporophores; after Sowerby[3]. *b*, Diagrammatic representation of a longitudinal section through a resupinate sporophore. *c*, The same, part of the sporophore is free from the substratum and bent over, protecting the hymenium, *h*.

are attractive objects under the microscope. In *Hymenochaete* resupination is not always complete, part of the sporophore being free from the substratum and bent over (fig. 259 *b*, *c*), protecting the hymenium which is then downwardly directed. *H. rubiginosa*[4], a common British species, is a cause of timber rot.

[1] Brooks and Sharples, 1923.   [2] Engler and Prantl, 1900.
[3] Sowerby, 1797.   [4] Brown, H. P., 1915.

In *Stereum*[1], another large genus, most of the species show the bracket form, with the sporophore partly or mainly free from the substratum, and the hymenium downwardly directed; the most elaborate forms possess a central stalk and a more or less funnel-shaped cap with the hymenium on its outer face. The conidial stage of *Stereum purpureum* is the cause of silver leaf disease[2], affecting rosaceous trees such as the apple and plum; the branches die, and on them the basidial fructifications develop. In *Sparassis*[3] the sporophore is richly branched, resembling a cauliflower or a bath sponge, and may reach nine inches in diameter; the hymenium is limited to the physiologically lower sides of the branches, different parts of the same side of a twisted branch bearing fertile or sterile hyphae according to their orientation.

Fig. 260. *Craterellus cornucopioides* (L.) Fr.; two sporophores bearing external hymenium.

In *Thelephora* the sporophore straggles over leaves and twigs, closely following the lie of the substratum (fig. 259 *a*); it may be more or less resupinate, may form overlapping shelves with the hymenium on the lower face, or may possess a central stem. The hymenium shows a tendency to become uneven, instead of smoothly spread, and its surface is often irregularly warted or arranged in shallow ridges.

Cyphella has a minute, pendulous cup, with the hymenium inside and either smooth or veined; *Craterellus* (fig. 260) shows a larger, funnel-shaped sporophore, with the hymenium external and often thrown into folds which suggest irregular gills.

The species of *Exobasidium*[4] are parasites on higher plants, the mycelium developing between the cells of the host and stimulating the formation of galls on stem and leaves. There is no definite sporophore; the genus may be primitive or reduced, and is

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[1] Ward, 1897; Mayo, 1925.
[2] Brooks, 1911–13; Brooks and Bailey, 1919; Brooks and Moore, 1926; Brooks and Storey, 1923.
[3] Cotton, 1911.   [4] Burt, 1915.

probably not closely related to the remaining Thelephoraceae. *Exobasidium Vaccinii*, on *Vaccinium Myrtillus* and other Ericaceae, is not uncommon, and may be recognised by the characteristic red or purple swellings induced on subaerial parts of the host.

Clavariaceae

The Clavariaceae are characterised by the erect sporophore, which may be simple or branched, and over all sides of which the hymenium is smoothly spread. In *Clavaria* (fig. 261), the so-called

Fig. 261. *Clavaria cardinalis* Boud. & Pat.; after Boudier[1].
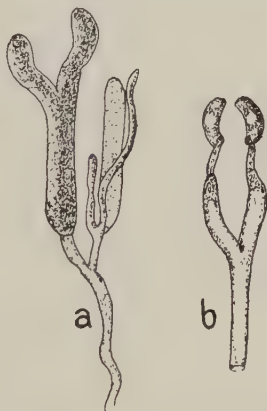
Fig. 262. *Dacryomyces chrysocomus* (Bull.) Tul.; *a*, young basidium with sterigmata, × 400; *Dacryomyces ceribriformis* Bref., *b*, upper part of mature basidium with two spores, × 359; after Brefeld[2].

fairy club, the sporophore is club-shaped or shows coral-like branching; it is usually white, buff or yellow and is from less than one inch to twelve inches high. Most species of *Pterula* have numerous, filiform branches, forming a brush-like tuft; *Typhula* consists of usually unbranched threads arising from sclerotia; and in *Pistillaria* the sporophore is a minute club, generally occurring on dead stems or leaves.

Calocera resembles a small *Clavaria* in habit, but differs in the gelatinous consistency of its sporophore, becoming horny when dry, and in the specialised type of basidium (fig. 262), which has two very long sterigmata, about half as wide at the base as the

[1] Boudier, 1905.   [2] Brefeld, 1884.

basidium itself, and bears only two spores. *Dacryomyces*[1] forms small, subglobose, gelatinous masses; it is included here owing to the similarity of its basidium to that of *Calocera*; both genera occur on dead wood.

HYDNACEAE

The salient character of the Hydnaceae is the arrangement of the hymenium over warts or spines of sterile tissue; these excrescences may be very long and pointed, resembling stalactites, or may be rudimentary in character; there is a transition also from crust-like, resupinate forms to forms with a stem and pileus and the general appearance of a toadstool. In some cases the protuberances covered by the hymenium are united to form irregular plates.

Among the commoner genera, *Phlebia* has a soft and somewhat gelatinous sporophore, erect or lying more or less flat on the substratum,

Fig. 263. *Hydnum repandum* (L.) Fr.; stipitate sporophore.

with the surface thrown into irregular wrinkles; in *Radulum* the sporophore is resupinate, but here the projections take the form of blunt fingers. In *Irpex* the irregularities of the surface originate as shallow pores and are later torn into narrow ridges and coarse teeth, and the sporophore, though mainly resupinate, may be partly free and bent over; in *Hydnum* the type of sporophore ranges from resupinate forms with outwardly directed teeth, through bracket-like species in which the teeth hang downwards, and are protected by the sterile tissue, to forms with a cap and central stalk (fig. 263); in all species of *Hydnum* the teeth are well-differentiated, awl-shaped, and distinct at the base.

AGARICACEAE

The Agaricaceae form a considerable assemblage of gill-bearing species most of which possess a cap and a central stem, though in some the stalk is lateral, and others are bracket-like in form; they are classified according to the colour of the spores (which may be

[1] Wager, 1914 ii; Buller, 1922 i.

white, pink, some shade of reddish brown, purple, or black), the shape of the gills, the shape of the cap, the method of protection of the young sporophore, and other details. From the evolutionary point of view they are all at much the same level of development; they may possibly have been derived from such forms as *Craterellus* or *Phlebia*, but do not appear to have given rise to any higher group, perhaps because they are well adapted to the environment in which they occur. It is a question whether some of the Polyporaceae or Gasteromycetales have reached a higher level

Fig. 264. *Panaeolus campanulatus* (L.) Quél.; longitudinal section through part of a young gill, showing young, binucleate basidia, basidia after the nuclei have fused, and basidia with sterigmata and four nuclei; the numbers indicate successive stages in development; somewhat diagrammatic, × 1000.

of development, but they are not likely to have been derived from the Agaricaceae, though they doubtless had common ancestors.

The gills, or lamellae, are arranged on the under side of the cap, or pileus. In symmetrical species the stalk, or stipe, springs from the middle of the cap, and the gills radiate between the point of its insertion and the outer edge of the pileus; shorter gills, starting from the edge, reach only part of the way towards the centre, thus filling the gaps between the outer ends of those which form complete radii. A section of the gill (fig. 264) shows a central trama of parallel or interwoven hyphae, the ends of which bend outwards to form the subhymenium and ultimately to give

rise to the basidia, paraphyses, and cystidia of the hymenial layer.
In some cases the developing gills are protected merely by the
curvature of the edge of the pileus and its contact with the stipe,
in others, as in the mushroom, a special weft of hyphae, the
velum partiale or **partial veil**, connects the edge of the
pileus with the stalk, and is torn apart when the pileus expands,

Fig. 265. *Amanita phalloides* Fr.; young and mature sporophores; after
Cooke.

leaving around the stipe a circular frill, the **annulus** or **ring**
(fig. 265). In addition to either of these methods a further pro-
tection is given in *Amanita* and a few other genera by the develop-
ment of a special membrane, the **velum universale** or **volva**,
which extends over the whole sporophore and within which de-
velopment takes place. The volva is ruptured by the elongation
of the stipe, torn fragments are carried up on the outer surface of

the enlarging pileus, but the greater part remains about the base of the stem (fig. 265).

The development[1] of the sporophore begins with the formation of a little knot of interwoven filaments; as growth proceeds the position of the fertile layer is early indicated by a ring of deeply staining hyphae; above this the tissue of the pileus grows rapidly; below, the growth of the region which will constitute the stipe ceases or is delayed; as a result an annular cavity is formed. This gill cavity is at first minute but rapidly enlarges as the pileus continues its growth, and into it push hyphae from the deeply staining layer, forming the gills; with the expansion of the pileus these are later carried into a horizontal position. There is a good deal of variation in detail between different species, and comparatively few have as yet been fully studied; in *Amanita*, for example, the ring of gill-producing tissue is lacking and the gills arise from isolated primordia, while, in forms without a partial veil, the gill cavity may be open from the first to the exterior. *Psalliota*, *Armillaria*, and other genera which do not show a volva at maturity may be enclosed during development by a weft of hyphae corresponding to the primordium of the universal veil but disappearing at an early stage.

Among the many species in this family, *Psalliota campestris*, the mushroom, is probably the best known; the stem is central, the spores are purple, and there is a well-marked partial veil. This fungus is extensively cultivated for food either out of doors or in caves or tunnels, the vast limestone caves beneath the suburbs of Paris being used for this purpose. There are many other edible forms among the Agaricaceae and their allies, but there are also many which are poisonous, and none should be eaten unless the species is definitely known. The most dangerous is *Amanita phalloides* (fig. 265), a white-spored, white or yellowish species with both a volva and a partial veil; it is probably responsible for ninety per cent. of the deaths due to fungi; a very small quantity can be fatal, and, even when death does not occur, great pain and long illness are inevitable. The related *Amanita muscaria*, the fly agaric, characterised by the red pileus to which white fragments of the volva adhere, is also poisonous, and an extract of the dried cap produces intoxication.

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[1] Atkinson, 1906, 1914, 1916; Fischer, 1909; Sawyer, 1917; McDougall, 1919; Walker, 1919; Moss, 1923.

Armillaria mellea, a white-spored form with a well-marked ring, and a conspicuous, brown, scurfy pileus and stalk, besides being a constituent of mycorrhiza[1], is a harmful tree parasite. Spores germinate on dead stumps, and in addition to producing fresh sporophores, send out interwoven strands of hyphae, the rhizo-
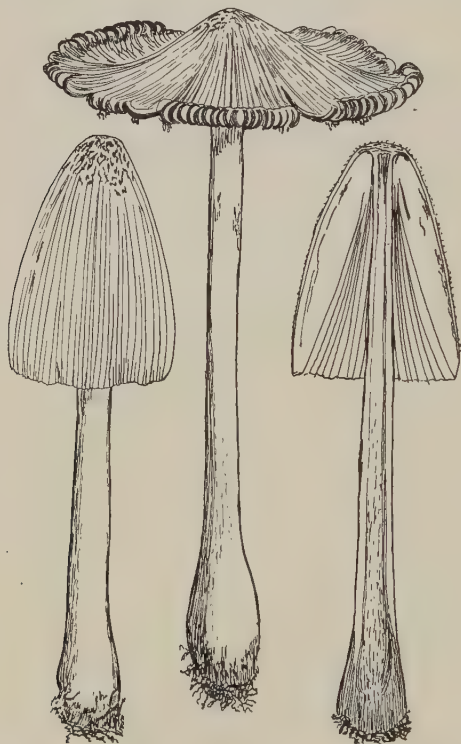
Fig. 266. *Coprinus aratus* Berk. & Br.; mature and nearly mature sporophores; after Cooke.

morphs, which are easily recognisable from their resemblance to black bootlaces. If, under circumstances favourable to infection, they come in contact with the roots of living trees, they force their way in, spreading to form a white, felt-like mycelium just inside the bark; the cambium is infected and the xylem and phloem attacked by way of the medullary rays, thus bringing about the death of the tree and the subsequent decay of the wood. The young

[1] Cf. p. 25.

rhizomorphs are luminous, as are the hyphae of some other Basidio-mycetes, and pieces of wood impregnated with them were formerly used as a source of light in places, such as barns containing hay, into which a torch could not be carried.

The genus *Coprinus*, the ink cap (fig. 266), is one of the com-monest forms with black spores; the spores are produced in succession[1], first from basidia at the edge of the cap, later from those progressively nearer the stem. As the spores are shed the gills undergo deliquescence or autodigestion, disappearing in the form of inky drops. Since the ripe spores are always just above the region of deliquescence, and therefore at the edge of the gill, they fall free in this genus even if the gill is tilted.

The curious genus *Secotium*[2], formerly referred to the Hymeno-gastraceae, should probably be placed in this family in the neigh-bourhood of *Psalliota*; the sporophore is surrounded by a thick volva or peridium which opens to disclose the much folded gills.

The species of *Nyctalis* are remarkable for being parasitic on other agarics, from the stalks and pilei of which they develop; they are disseminated not only by basidiospores, but by conidia produced on the surface of the cap.

Among the excentric species *Lentinus*[3] has a funnel-shaped sporophore; *L. lepideus*[4], to the reactions of which reference has already been made, is a common cause of damage to railway sleepers and other wooden structures. *Schizophyllum* has a lateral stem or none, and, in *S. commune*, shows a unique method of protection of the hymenium; each gill is divided in the plane of its most extended surface, and, if desiccation sets in, the liberation of spores ceases, and the two halves curl one away from another till, when the sporophore is quite dry, segments of the larger gills completely cover the smaller ones. In this condition the fungus can retain its vitality for years. *Pleurotus* and *Lenzites* may be bracket-shaped or resupinate; in *Lenzites* the gills are some-times united to form pores, and a connection with *Daedalea* may be surmised.

[1] Buller, 1909 ii.   [2] Conard, 1915.   [3] Johnson, 1920.
[4] Buller, 1905, and cf. pp. 37, 38.

POLYPORACEAE

The Polyporaceae, as their name implies, are characterised by the presence of numerous pores, the cavities of which are lined by the hymenium. The pores may be merely shallow pits, as in the resupinate genera *Merulius* and *Poria*; they may be wavy and laterally elongated, sometimes almost resembling gills, as in species of *Daedalea*, or, as in *Boletus*, *Polyporus*, *Polystictus*, *Fistulina* and *Fomes*, they may form long, narrow tubes, closely crowded together, so that the open ends, through which the spores escape, occupy the fertile surface of the sporophore.

In *Boletus* there is a central stem and a symmetrical pileus, usually large and very fleshy; the cap and pores are often bright coloured, and, in several species, the flesh turns blue when exposed to the air owing to the presence of a phenol known as boletol, together with the oxidising agent, laccase, its co-enzyme, which is a compound of manganese, and suitable alkaline salts[1]. In *Polyporus* a central stem is sometimes found, but most of the species are bracket-shaped, growing out of stumps or tree trunks; in the latter instance they are often destructive parasites, inducing heart rot; in several cases the spores enter through wounds[2]. *Polystictus* differs from *Polyporus* in its thin flesh and velvety upper surface, and *Fomes* in the stratification of its tubes. This stratification is due to the fact that each spring a layer of sterile tissue closes the old tubes, and on it the tubes of the current year arise; *Fomes officinalis*, so called from its use as a purgative by the ancient Greeks and Romans, may show as many as forty-five strata, indicating an age of forty-five years. *Fomes applanatus*[3], a wound parasite, is responsible for the decay of large quantities of wood, since it attacks all sorts of deciduous trees and several coniferous species, both in the living state and after death; delignification is brought about, and is followed by progressive solution of the resultant cellulose wall[2]. In *Fistulina*, a bracket form, the tubes containing the hymenium are separate one from another; *F. hepatica*, known as the beef steak fungus, is edible; it occurs mainly on old oak trunks.

Merulius lacrymans and *Poria vaporaria* are causes of dry rot, a most destructive affection of woodwork in badly ventilated houses; not only do the hyphae penetrate into and destroy the wood, but,

[1] Bertrand, 1902.   [2] Buller, 1906; Brooks, 1909, 1925.
[3] White, 1919.

under dry conditions, when this is not possible, they spread in strands or sheets over the surface, and even over brickwork and bell wires till a fresh supply of moist wood is reached and attacked. Infection may often take place in the timber yard, before the wood is used. Spores of *Merulius* are stated to germinate readily on wood attacked by the thelephorous genus *Coniophora*[1], or other fungi, and *Coniophora*, in turn, which is incapable of dealing with dry wood, can flourish in the presence of the moisture exuded by *Merulius lacrymans*.

Daedalea may be bracket-shaped or resupinate; in this genus, with its pits intermediate between rudimentary gills and pores, we have a suggestion of the origin of the higher members of the family, and possibly of a relationship between their ancestors and those of the Agaricaceae. *Daedalea*, in its turn, may have been derived from a form like *Poria* or *Merulius*, or like the young sporophore of *Irpex*, and these are not remote from the wrinkled hymenium of *Phlebia*.

GASTEROMYCETALES

The Gasteromycetales include between 600 and 700 species characterised by the retention of the fertile tissue within a closed peridium, corresponding to the volva of some of the Agaricaceae, until after the spores have reached maturity. The peridium may be of one, two or three layers; where there is more than one, the term **exoperidium** is applied to the outer, and **endoperidium** to the inner. The contents of the peridium are often described as the **gleba**; they may form a continuous mass, or a series of closed chambers, or may be separated by a weft of thickened hyphae, forming accessory walls, into one or more **peridiola**. Usually the ripening of the spores is followed by the deliquescence of the basidia and other cells of the gleba, but in several species long, simple or branched hyphae remain unaltered; they are known as the **capillitium** and may help in the distribution of the spores.

In subterranean forms the peridium is never ruptured, but, when the spores are ripe, the sporophore emits a strong smell by which rodents are attracted; the sporophore is eaten and the spores distributed after passing through the alimentary canal. It is

[1] Falck, 1912.

interesting to note the close parallelism between the distribution of these forms and of the subterranean Ascomycetes.

In the majority of subaerial species spore dispersal is by wind; after deliquescence the gleba dries to form a powdery mass; the peridium is ruptured and the spores escape. In *Lycoperdon*, the puffball, the emission of spores depends on contacts or disturbances of the air due to passing animals; in *Bovista* the mature sporophores break readily away from their support, and are blown about by the wind, distributing spores as they go; in *Scleroderma* the peridium opens and the spores are blown out in dry weather and washed out in wet.

In the Phallaceae and some other members of the alliance, the sporophore remains underground during development; when maturity is reached the peridium is ruptured and the rapid elongation of the stalk carries the hymenium into the air. In the stinkhorn, *Phallus*, and its allies, flies are attracted by the strong smell and sweet taste of the mucilage accompanying the spores, and the latter are carried away on their legs or pass through their alimentary canal. In *Sphaerobolus* the whole contents of the peridium are shot out by means of a mechanical device.

In correlation with these methods of distribution the spores on a gasteromycetous basidium are often crowded together, the sterigmata are either short, as in species of *Scleroderma*, or long and very thin, as in *Lycoperdon*, and are sometimes variable in length. The basidium and sterigma, in fact, play no part in the distribution of the spores, as in the Hymenomycetales, but only in their production.

All the Gasteromycetales are saprophytes, though the mycelium of some may form a constituent of mycorrhiza; in none of them are conidia produced; in most species the vegetative filaments are woven into rhizomorphs on which the sporophores are formed.

Little can be said of the interrelationships of the members of this alliance, or of their probable origin, though, from the similarity of the basidium and general arrangement, it would appear that they, or some of them, and the Hymenomycetales had a common ancestor; moreover, if the presence of clamp connections can be trusted as an indication of specialised nuclear conditions, it would appear that they diverged after this state of affairs had been established. The Nidulariaceae and Phallaceae, in particular, show a high

degree of specialisation, and there is some reason to think that the Phallaceae may have been derived from the Hymenogastraceae.

The alliance may be subdivided as follows:

Developed underground

 The whole sporophore remaining underground   HYMENOGASTRACEA

 The hymenium raised on a stalk or lattice at maturity   PHALLACEAE

Developed above ground

 Peridium opening at maturity to emit clouds of spores

  Capillitium present   LYCOPERDACEAE

  Capillitium absent   SCLERODERMACEAE

 Peridium opening to disclose one or more peridiola   NIDULARIACEAE

HYMENOGASTRACEAE

The members of the Hymenogastraceae are subterranean species, occurring usually under trees, and having possibly a symbiotic relation with the roots of the latter; the mycelium spreads through the neighbouring humus, sometimes forming rhizomorphs, from the tips of which the oblong or globose sporophores arise. In *Gautieria* (fig. 267) and *Hysterangium* the medulla of the rhizomorph is continuous with the columella of the sporophore; the fertile tissue originates from this strand (fig. 268), grows in the form of irregular fingers towards the periphery, and pushes outward the peridium. In *Hymenogaster* the fertile tissue

Fig. 267. *Gautieria morchellaeformis* Vitt.; sporophore in longitudinal section showing rooting hyphae and columella; after Vittadini.

originates at the periphery and grows inwards (fig. 270); in either case the strands branch and anastomose and so form the chambers of the gleba. In *Rhizopogon*, on the other hand, the developing gleba is continuous and shows dense areas alternating with others where the hyphae are loosely interwoven; chambers are formed by the tearing apart of the latter[1].

At maturity the gleba never becomes powdery; its general appearance is very like that of *Tuber* and of some of the species

[1] Rehsteiner, 1892.
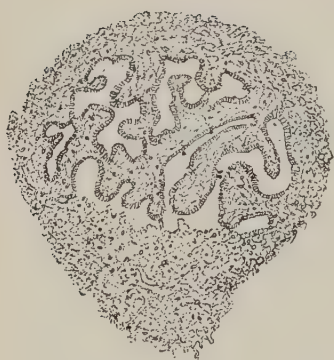
Fig. 268 a. *Hymenogaster decorus* Tul.; young sporophore with processes clothed by fertile tissue growing inwards from the periphery, × 28; after Rehsteiner.

Fig. 268 b. *Hymenogaster decorus* Tul.; as a but younger, × 28; after Rehsteiner.
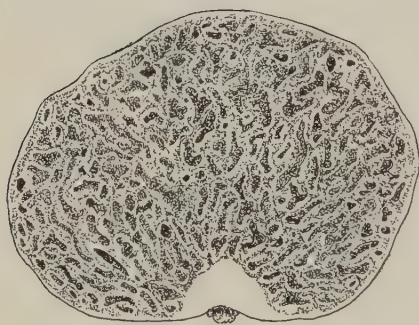
Fig. 269. *Hymenogaster tener* Berk.; mature sporophore in longitudinal section; after Tulasne[1].
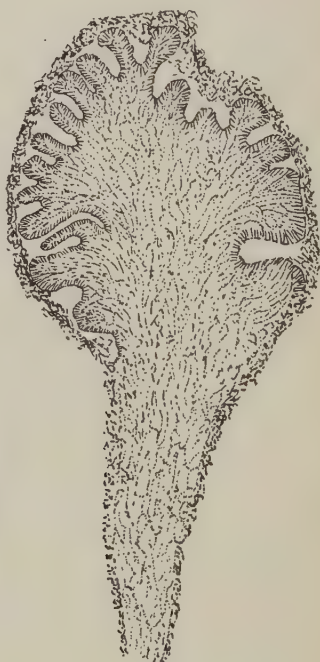
Fig. 270. *Hysterangium clathroides* Vitt.; young sporophore in longitudinal section, with processes clothed with fertile tissue pushing out from columella, × 28; after Rehsteiner.

[1] Tulasne, 1851.

known as false truffles; as in the truffle, the peridium is thick, and, in *Rhizopogon*, three layers can be distinguished. In *Hysterangium*, *Melanogaster* and *Hymenogaster* the sporophore has a sterile base (fig. 269), in *Rhizopogon* and other genera the whole contents of the peridium are fertile.

PHALLACEAE

In the Phallaceae[1] the peridium is ruptured when the spores reach maturity and the gleba is carried up on a specially differen-
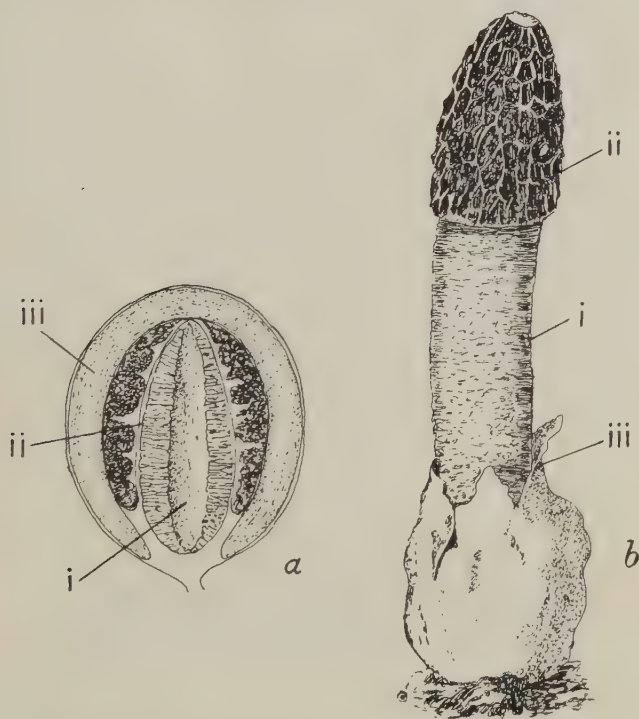
Fig. 271. *Phallus impudicus* L.; *a*, young sporophore in longitudinal section, × ½; after de Bary; *b*, older sporophore after the peridium has been ruptured and the stipe elongated; after Fischer[2]. i, stipe, ii, pileus bearing gleba, iii, gelatinous layer of peridium.

tiated receptacle. In *Phallus impudicus*, known from its smell as stinkhorn or dead men's fingers, the exo- and endoperidium are

[1] de Bary, 1887; Burt, 1894, 1896 ii, 1897; Petch, 1908; Fischer, 1910, 1923 i.
[2] Engler and Prantl, 1900.

tough, white membranes, between which is a gelatinous layer de-
rived, at an early stage, from the disintegration of the hyphae; the
exoperidium is continuous at the base with the receptacle, a sterile
column which runs up the middle of the gleba, forming a hollow
stipe filled with mucilage and developing elaborately chambered
walls. The fertile tissue of the gleba arises from the peripheral

Fig. 272. *Dictyophora phalloidea* Desv.; mature sporophore; after Möller.

zone just within the endoperidium; it is differentiated into cham-
bers and supported on a tough membrane (fig. 271 ii) which later
constitutes the pileus; the walls of the trama early become gela-
tinous. During development the sporophore is usually hidden
under humus; it attains the size and shape of a hen's egg and is
attached to a conspicuous, white rhizomorph, which may be traced
for a considerable distance in loose soil. When the spores have

ripened, the gleba breaks down, forming a viscid, olive-green slime; the elongation of the stipe begins (fig. 271 b); the peridium is torn; and the pileus, with the viscid spore mass, is carried up into the air. Given adequate water supply, the full size is reached about half an hour after the rupture of the peridium. The characteristic smell and sweet taste of the disintegrated gleba attract bluebottles and other flies and by them the spores are distributed.

Mutinus[1] is very similar in structure to *Phallus*, but the sporophore is smaller, and the pileus is adherent to the stipe. In the genus *Dictyophora* a white network hangs below the pileus (fig. 272) and corresponds[2] to a rudimentary tissue between the pileus and stem of *Phallus impudicus*, which, in the latter, never reaches full development. The colours are brilliant, the pileus being snow-white, pink, orange or yellow, the mycelium sometimes violet, and the network white.

In *Lysurus* the pileus is replaced by five or six lobes, and in *Aseroë* by a lobed disc; in both cases the spore mass is situated on the inner, or upper face. This is also the case in some of the tropical genera and in *Clathrus*, where the re-

Fig. 273. *Clathrus cancellatus* Tour.; mature sporophore; after Rolland.

ceptacle (fig. 273) has the form of a wide-meshed lattice, usually red in colour and contrasting with the white peridium.

In the developing sporophore of *Phallus* and its allies the basidia are peripheral in origin and face towards the axis; in *Clathrus*, and in other forms bearing the spore mass on the inner side of the receptacle, the basidia arise as outgrowths from the central tissue and are directed towards the periphery; these arrangements correspond to the conditions in *Hymenogaster* and *Hysterangium* respectively, and suggest that the Phallaceae fall naturally into two divisions with a separate origin among subterranean forms.

[1] Burt, 1896 i; Fischer, 1923 i.   [2] Atkinson, 1911.

LYCOPERDACEAE

The members of the Lycoperdaceae are distinguished by the peridium of two layers, the outer of which may be further differentiated, and by the presence of a capillitium among the spores; the chambers of the gleba are produced, as in *Rhizopogon*, by the tearing apart of the tissue during growth.

Lycoperdon, the puffball, has a well-marked sterile base, and a capillitium of irregularly branched threads which, in *L. pyriforme*
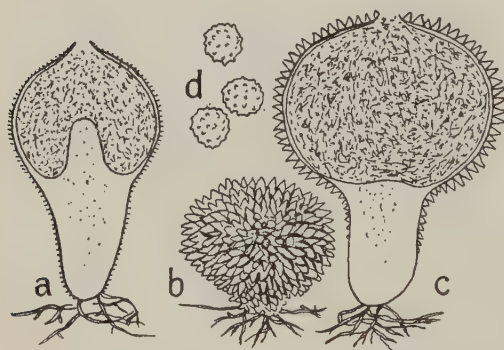
Fig. 274. *Lycoperdon pyriforme* Schaeff.; *a*, sporophore in longitudinal section showing columella, × ½; *Lycoperdon echinatum* Pers., *b*, young sporophore, × ½; *c*, mature sporophore in longitudinal section, × ½; *d*, spores, × 750; all after W. G. Smith.

Fig. 275. *Tulostoma mammosum* Fr.; sporophore in longitudinal section, × ⅔; after W. G. Smith.

(fig. 274 *a*) and others, forms a dense central mass, the columella, remaining after the spores have blown away. The outer layer of the peridium is warted or spiny, and may disappear entirely, especially in wet weather, as the sporophore ripens; the endoperidium opens apically by a small, round hole when the spores are ready for dispersal. *Queletia* is somewhat similar, but the sterile base is elongated to form a stout, scaly stipe, and the endoperidium opens irregularly. *Tulostoma* (fig. 275) also is stalked, and resembles a small puffball mounted on a stem. In *Bovista* the sterile base is absent, the exoperidium is papery and smooth, breaking away in irregular fragments, or remaining as a cup about the lower part of the fruit; the endoperidium opens by a definite pore.

In *Geaster* the young sporophore is more or less globose; the

exoperidium is differentiated into a mycelial, a fibrous and a fleshy layer[1] and splits into pointed segments which spread outwards (fig. 276 *a*), leaving the gleba surrounded by the endoperidium which opens by a small apical pore, or, in the section of the genus sometimes separated as *Myriostoma*, by several apertures, giving a pepper-pot effect. The endoperidium may be raised on a stalk above the stellate segments of the outer layers. In some cases the two layers of the exoperidium may separate (fig. 276 *b*), the outer remaining concave and the inner becoming convex.
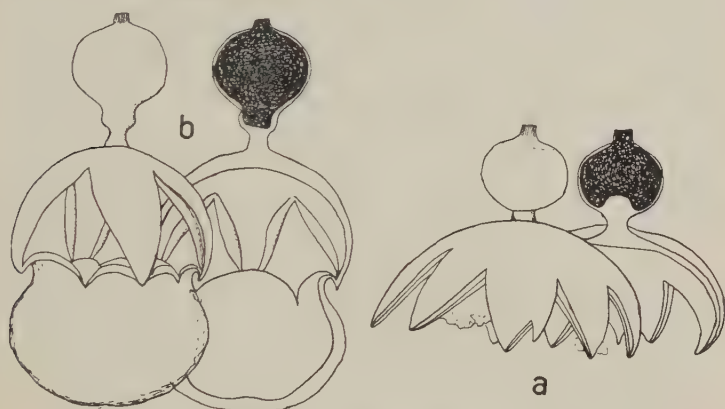
Fig. 276. *Geaster Berkeleyi* Mass.; *a*, mature sporophore entire and in section; *Geaster fornicatus* Fr., *b*, mature sporophore entire and in section; × ⅖; after W. G. Smith.

The sporophore of *Battarrea* develops underground; as in *Geaster* the exoperidium opens at maturity, but here the sterile base or stalk of the endoperidium is carried to a height of eight to fourteen inches, and is afterwards ruptured, exposing the spores.

SCLERODERMACEAE

In the Sclerodermaceae the gleba is enclosed in a thick peridium, consisting of a single layer; and the sporophore is narrowed below to form a sterile base. At maturity the peridium splits irregularly or partly disintegrates, liberating the spores. The gleba is divided by sterile tracts, and the capillitium is absent or rudimentary.

The species of *Scleroderma* are almost sessile, and are thus distinguished from the members of the genus *Polysaccum*, in which

[1] Cunningham, 1927.

a definite stalk supports the fertile region. In *Polysaccum* the areas of the gleba, separated by sterile tracts, are ultimately rounded off to form peridiola, whereas, in *Scleroderma*, the whole gleba becomes powdery.

Scleroderma vulgare (fig. 277), sometimes known as the vegetable tripe, occurs very commonly under trees; it has a thick,
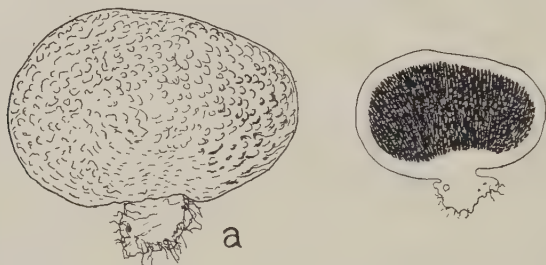
Fig. 277. *Scleroderma vulgare* Hornem.; *a*, mature sporophore; *b*, younger sporophore in section; × $\frac{2}{5}$; after W. G. Smith.

white or pale brown peridium, externally roughened by scales or warts; the black or purplish gleba is used to adulterate *pâté de foie gras* and similar preparations of which the French truffle, *Tuber macrosporum*, is an ingredient.

NIDULARIACEAE

The Nidulariaceae are a curious little group of plants, sometimes known as bird's nest fungi. The peridium opens wide at maturity, exposing the gleba, which is divided into a number of peridiola, each surrounded by a thick wall, and resembling a clutch of eggs in a nest. Each peridiolum is hollow, the basidia projecting inwards from the wall, which, developmentally, is a thickened layer of

Fig. 278. *Crucibulum vulgare* Tul.; group of sporophores, nat. size; after Fischer[1].

the trama, the whole peridiolum corresponding to a single cavity of the gleba. Between the peridiola the mycelial threads, as

[1] Engler and Prantl, 1900.

growth proceeds, become gelatinised and break down, leaving the peridiola exposed. In *Nidularia* the peridium is a single, thin membrane, opening at maturity to form a cup in which the peridiola lie free and enveloped in mucilage. In *Crucibulum*[1] (fig. 278) the peridium is differentiated into two layers, a loosely woven exoperidium, bearing long hairs, and an endoperidium of more or less gelatinised hyphae. Before maturity the peridium opens, exposing the remains of the undifferentiated tissue of the young sporophore, which conceals the peridiola (fig. 279 *b*) and is known as the **epiphragm**; it eventually becomes gelatinised and torn apart. On the flattened side of each peridiolum (fig. 280), next the peridium, is a median depression, the centre of which is occupied by a nipple-

Fig. 279. *Crucibulum vulgare* Tul.; young and mature sporophores in longitudinal section, × 3; after W. G. Smith.

shaped mass of coiled and twisted hyphae, continued outwards as a sinuous thread, enclosed in a loose bag of partly gelatinised hyphae, and attaching the peridiolum to the peridium. When these hyphae and the surrounding mucilage are moistened they swell, and the sinuous thread becomes softened and can be pulled out to a length of three or four centimetres. It is difficult to indicate any function fulfilled by this curious structure, but it has been suggested that the mucilaginous threads may assist in dispersal by animals.

In *Cyathus*[2] (fig. 281 *a*) the peridium is differentiated into three layers, a middle, pseudoparenchymatous zone being developed between the exo- and endoperidium which correspond to those of *Crucibulum*; the epiphragm consists of the ground tissue of the gleba. The stalk of the peridiolum is at first 2 mm. long and is divided by a slender, middle region into upper and lower portions (fig. 281 *b*); the middle and lower segments are composed of narrow, branching hyphae, which become tough and elastic when moist; the upper segment, nearest the peridiolum, forms a bag, similar to that in *Crucibulum*, in which is coiled a slender thread (fig. 281 *c*) some three centimetres in length and attached at its upper end to the peridiolum. When the walls of the bag are ruptured, the whole stalk may be drawn out to a length of as much

[1] Molliard, 1909; Walker, 1920.   [2] Walker, 1920.

as eight centimetres; the hyphae of the extensible tissue are thick-walled, their lumina having almost disappeared.

The genus *Sphaerobolus* differs from the other members of the family in having a single peridiolum (fig. 282 *a*, *b*) and in the function and elaboration of the peridium. The exoperidium is

Fig. 280. *Crucibulum vulgare* Tul.; section through part of a young sporophore, showing the developing peridiola; after Sachs.

white and floccose; the endoperidium consists of an external, fibrillar, and an internal, collenchymatous zone; the cells of the latter are large and radially arranged, and their contents are rich in glycogen. The whole peridium, when mature, divides into six or seven stellate lobes, exposing the peridiolum; growth continues in the collenchymatous zone and, as the other layers do not grow

with it, a state of tension is produced and at last brings about the separation of the collenchymatous layer from the exoperidium except at the tips of the lobes; it becomes arched outwards, carrying
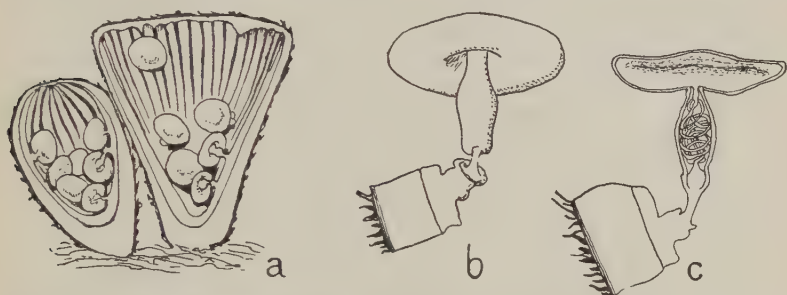
Fig. 281. *Cyathus striatus* Hoffm.; *a*, young and mature sporophores in longitudinal section, × 3; *b*, *c*, single peridiola entire and in section, × 10; after W. G. Smith.
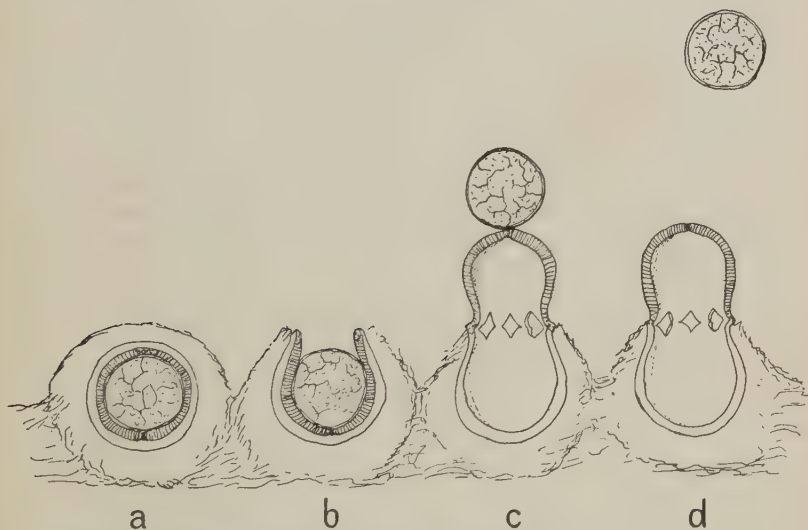
Fig. 282. *Sphaerobolus stellatus* Tode.; stages in the liberation of the peridiolum, × 12; after W. G. Smith.

with it the fibrillar layer. If this takes place slowly, the peridiolum remains poised on the arch (fig. 282 *c*); if, as usually happens, the process is sudden, the endoperidium changing its position with a jerk, the peridiolum is shot away (fig. 282 *d*) to a distance of as

much as fourteen feet[1], and, being mucilaginous, adheres to an object on which it alights. Energy appears to be obtained by the transformation into sugars of the glycogen of the collenchymatous layer, with consequent increase of osmotic pressure; the change is gradual if the temperature is low and the light dim, but, at a temperature of $32.5°$ C. and in bright light it takes place rapidly and violent ejection results. Internally the peridiolum shows a number of imperfectly divided chambers, and thus differs from the peridiola of *Cyathus* and its allies; after ejection the peridiolum does not break up but puts out a mass of germ tubes; these arise from short, cylindrical cells occurring in rows within the gleba; the basidiospores have not been observed to germinate.

[1] Walker and Andersen, 1925.

FUNGI IMPERFECTI

Many thousands of fungi are known in which conidia are the characteristic unit of multiplication, though in some oidia and chlamydospores may be found. Neither sporangiospores, ascospores nor basidiospores are produced, nor are sexual organs found, and accordingly such forms cannot be referred to any of the main subdivisions of the fungi from which they are probably derived, and of which they may be regarded as reduced or incompletely known representatives, showing only a gametophytic mycelium with accessory organs of multiplication. These species are described as *Fungi imperfecti*. They are an artificial assemblage, and many of the genera include members which are grouped together owing to a resemblance in their method of growth, but are not related; these are known as **form genera**. Thus the form genus *Oedocephalum* contained species which have now been shown to be stages in the life history of Phycomycetes, Ascomycetes and Basidiomycetes, as well as others which are known to produce only the *Oedocephalum* form; *Botrytis* is a conidial phase in the development of such Ascomycetes as *Sclerotinia* and such Basidiomycetes as *Hydnum omnivorum*[1], while other species of *Sclerotinia* have conidia of the *Monilia* form, which are thus actually more closely related to species of *Botrytis* than species of *Botrytis* are one to another. Again the hyphomycetous genera *Penicillium* and *Coremium* indicate different methods of growth of the same fungus; *Penicillium* has the characteristic form of the conidial stage belonging to the plectomycetous fungus of that name, and most of its species are probably members of the Aspergillaceae which produce no sexual stage or ascus fructification under ordinary conditions; in *Coremium* conidiophores, in no way different from those of *Penicillium*, are bunched together in response to the peculiarities of the environment.

The occurrence of similar systems of branching in the conidiophores of unrelated forms is doubtless due to the fact that each has reached in the course of evolution a similar solution of a common problem, involving the efficient exposure of the spores to the air for dispersal. The conidiophores of *Botrytis*, the sporangiophores of *Thamnidium* and *Blakeslea* among Zygomycetes, and the corresponding structures in the Peronosporaceae may be compared from this point of view. Many of the *Fungi imperfecti*,

[1] Shear, 1925.

under circumstances favourable to their growth, increase with great rapidity and some are the cause of serious plant disease.

In classifying the *Fungi imperfecti* it is convenient to include with them the conidial forms of fungi, the other phases in the life history of which are known, and to subdivide them according to the peculiarities of their conidial development and without reference to any sexual stage. Such a grouping is purely artificial; it is a key, not a natural system, and has no relation to origin or evolution, only to form. So long as different spores of the same fungus are developed in response to different conditions of environment it is likely to prove a valuable adjunct to attempts at a natural classification.

On this basis the Sphaeropsidales include forms with short, simple or branched conidiophores contained in flask-shaped receptacles known as pycnidia. The pycnidia may arise directly from the mycelium as in *Phoma*, or may be produced in or on a stroma. When mature the conidia escape through a definite pore, the ostiole, or are set free by a rent in the pycnidial wall; they are often held together by mucilage, forming long, twisted strings. Pycnidia are found in several members of the Pyrenomycetes, and it is possible that many of the Sphaeropsidales belong to that class.

In the Melanconiales, also, the conidiophores are short, but in this group there are no pycnidia. The species are parasitic, or are saprophytes on dead plants, and a more or less definite stroma is developed below the epidermis or periderm of the host, which is ruptured when the conidia are mature. The arrangement recalls the conidial stage of *Rhytisma* as well as of other Discomycetes.

The Hyphomycetales possess neither pycnidia nor stromata; they include most of the saprophytic *Fungi imperfecti*, as well as many parasites. The conidiophores are simple or branched, and may arise singly from the mycelium or be assembled in a brush-like coremium, or in a hemispherical sporodochium. The conidia are borne singly or in groups or chains, and the whole structure is usually exposed on the surface of the substratum. Similar growth forms are found in all the great groups of fungi.

These distinctions may be summarised as follows:

    Conidiophores not grouped in pycnidia
            Stroma not present   HYPHOMYCETALES
            Stroma present   MELANCONIALES
    Conidiophores grouped in pycnidia   SPHAEROPSIDALES

MYCOLOGICAL TECHNIQUE

As the study of fungi involves cultivation on artificial media and special applications of micro-technique, a record of some of the methods employed by the authors and their colleagues may be useful; by no means all of these are original, but most of them have been tested by several years' work.

Fungi, like all other organisms, should be studied as far as possible in their natural habitat, but the mycelia of many of the smaller species are so intermingled under these circumstances that the stages of their development cannot with certainty be separated, and the use of pure cultures becomes essential. The common obligate saprophytes and such facultative saprophytes as *Pythium* and *Phytophthora* grow readily in culture. Many coprophilous forms develop freely on sterilised dung or dung agar to which scraps of grass or filter paper have been added. Aquatic species may often be obtained by throwing dead insects into pond water.

In the laboratory fungi are most conveniently grown in Petri dishes; tall species may be grown in beakers covered with half a Petri dish, or in conical flasks plugged with cotton wool; cultures may also be made in test tubes containing a suitable medium; these cultures are useful for retaining a stock of a fungus, but they are inconvenient for purposes of examination.

Isolation. Isolation of a tall species is usually easy, as a platinum wire can be thrust among the spores, or, as in *Mucor*, a sporangium can be pinched off with sterilised forceps; subsequent transfer to a medium usually gives a clean culture. When a mixture of low-growing species is to be sorted out, the material is examined and the spores distinguished; either a single spore is isolated, or a few spores taken up in sterilised water in a sterilised pipette, and spilled on to prepared media; where bacteria are likely to be troublesome the medium is slightly acidified with citric acid. As soon as growth is visible to the naked eye, the colonies are cut out with a hot scalpel, and separately transferred to fresh media; it may be necessary to make several transfers before a clean culture

is obtained. If bacteria are present, the hyphal tips should be alone transferred, as they are usually in advance of the film of bacteria.

Solid Media. For rough cultures of *Mucor* and *Rhizopus* it is only necessary to scatter a little dust upon a slab of moist bread. This is placed under a bell jar, and, at ordinary temperatures, sporangia will be present in about a week. If the bread is left for a longer period, the Mucors disappear and Aspergillaceae and *Fungi imperfecti* may be obtained. Dung treated in similar fashion often yields a number of interesting forms, including *Mucor*, *Piptocephalis*, *Pilobolus*, various Ascomycetes and later, Basidiomycetes.

For more critical work, fungi are isolated from rough cultures and grown in Petri dishes, using a medium based on agar-agar.

A combination of the liquor of boiled potatoes with agar will support the growth of most of the saprophytes and some parasites found on plant material; coprophilous species usually flourish best on an appropriate dung agar; prune agar is of use in obtaining the perithecia of *Eurotium herbariorum*; for a fungus being brought into culture for the first time, it is well to try several media, including some made up from the substratum on which the fungus is usually found, with or without mineral salts. The methods of preparation given on p. 333 can be applied to a number of other substances.

Among synthetic mixtures Claussen's medium has been found useful in obtaining ascocarps of some of the Ascomycetes; two dishes are used, half of a small Petri dish being placed within a complete larger one. An agar made up with mineral salts and inulin is placed in the inner dish, while the annular space between the walls of the two dishes is supplied with a medium containing the same salts, but no inulin. The inner dish is inoculated, and fruiting occurs when the mycelium has grown into the outer dish. There must be plenty of space between the rim of the inner dish and the lid of the outer, and the spread of the fungus is facilitated if the inner dish is filled nearly full.

The medium appropriate to the outer dish can be used alone and gives fair results, but medium No. 6 on p. 333 has been found more effective. Often a synthetic medium is of value in obtaining stages in the life history of a refractory species; in such cases a start is made with one of the known media and the requisite modifications are determined by experiment.

While tap water and, except in the case of synthetic media, approximate quantities can be used if the intention is simply to cultivate the fungus or to study its development, for physiological work pure chemicals are required and must be made up with distilled water, and with due regard to accuracy in weighing. Care is needed, that only one of the substances in the medium, or one of the external conditions, should be altered at a time.

Liquid Media. If agar be omitted from the media just described, nutrient solutions are obtained; these are sterilised in flasks, and support the growth of a number of fungi.

Sterilisation. If Petri dishes are to be used, the medium is poured into flasks which are then plugged, and placed, with the required number of dishes, in a cold autoclave. Heat is applied, and, when steam issues freely from the valve, the latter is closed and a pressure of thirty pounds is maintained for about twenty minutes. The gas is then turned out, and, as soon as the gauge has fallen to zero, the valve of the outlet pipe is cautiously unscrewed. The Petri dishes when removed from the autoclave are placed flat on paper, and at once poured. This is done by lifting the lid of the dish sufficiently to allow the entrance of the neck of the flask containing the medium, pouring in enough to make a layer 5 mm. deep, and shutting down; it is sometimes desirable to pour in less, in order to get a shallow layer of medium which will allow of the examination of the culture through the bottom of the dish. It is well to avoid a draughty place for this operation, and the comfort of the operator will be increased by the use of a pair of thick woollen gloves. The plates are allowed to cool, and, when the medium has set, may be inoculated. If time permits it is better, before inoculation, to incubate the plates at 20° C. for three days or so. This dries off the water of condensation and allows time for contaminations introduced during pouring to become visible; contaminated dishes should be rejected.

Inoculation. In many cases, inoculation is performed by means of a piece of platinum wire set in a glass rod. The wire is heated in a flame, and, as soon as it is cool, pushed rapidly among the spores of the fungus, and, as quickly, through a narrow chink between the sides and lifted lid of the prepared dish, into the centre of the medium. It is best to avoid opening a dish more than once for this purpose; when an inoculation has been made, the

dish should be put aside and opened no more until the fungus is to be examined. When material is available a number of cultures of the same fungus should be made at the same time, and, unless there is good reason to the contrary, once a dish has been opened for examination, its contents should be preserved in a suitable fluid, or thrown away. In the event of a culture developing unwanted fungi, the colonies may be removed by the use of a hot scalpel, and this should be done before the intruders form spores.

Some fungi, such as *Phytophthora* and *Basidiobolus*, often do not form spores in large numbers. For their transfer, a piece of the medium, bearing the fungus, is cut out with a hot scalpel and rapidly carried to a fresh dish. The lid of the latter is opened only sufficiently to permit the introduction of the scalpel and its load, and, if the portion of inoculum is dropped on the way, or touches the outside of the dish, it is rejected, the scalpel reheated, and a fresh portion transferred. Scrupulous care is taken to avoid the introduction of anything except the fungus and the piece of substratum, and if it is suspected that extraneous material has been introduced, the dish is marked and specially watched.

Tube and Flask Cultures. When tubes and flasks are to be prepared for cultures, the medium is made up as for dishes, but it is usual to sterilise in the flask or tube. Accordingly, the agar is melted by heating, the whole well shaken, and a sufficient quantity of the medium poured into each vessel, care being taken to avoid wetting the mouth and sides. The receptacles are loosely plugged with cotton wool, and sterilisation is carried out. When removed from the autoclave, tubes are placed in a slanting position until cool, so that the medium sets in a slope. It is well to incubate for several days, in order to dry the plugs and give intruders an opportunity to reveal their presence. Inoculation is carried out as with dishes, but, before the plug is removed, its upper part is passed through a flame; the plug is lifted between the fingers so that it stands out from the back of the hand, and it is so held whilst inoculation is performed. The lower part of the plug should be passed through a flame before being replaced.

Single Spore Cultures. Two methods have been found simple and useful.

In one, a dummy objective fitted with a small sharp-edged tube in place of the lens, is attached to the microscope. The spores are spread thinly in a little water on stiff agar, and the surface examined with a 2/3″ objective. A spore lying at some distance from its neighbours is centred under the objective, the tube of the microscope is raised, the dummy objective swung into position, and carefully racked down until a circular cut is made in the agar. A second examination is made with the 2/3″ objective to ensure that the circle is around the spore, and the piece of agar is taken out on a sterile platinum wire, and quickly transferred to a Petri dish.

The second method depends on dilution. A quantity of spores is shaken up in sterile water, and small drops of the suspension are examined, being taken with a fine pipette which is heated between each drop. If the drop contains several spores, further dilution is needed; dilution is continued until about half the small drops contain one spore, the remainder, none. When the suspension is of the necessary strength, a drop is squirted on to the under side of a small piece of heated cover glass, suspended over a hole 3/16″ diameter, in a piece of hot sheet brass. Rapid examination is made, and, if a spore is present, the glass with its drop is transferred with hot forceps to a culture dish.

MICROSCOPIC EXAMINATION

Examination. The preliminary examination of the larger fungi, with or without a hand lens, requires no special comment; a similar examination of living micro-fungi should whenever possible be undertaken under a one inch, or, if a one inch is not available, a two-thirds objective. For this purpose the material is mounted on a slide, its long axis lying by preference parallel to the

Fig. 283.

glass, and the slide is placed on a piece of cardboard or paper which is twice folded (fig. 283) so that its upright sides reflect the light. Half a post card is just the right size for this purpose. The source of illumination, and, if necessary, a bull's eye condenser are so arranged as to throw light downwards on the specimen, which is then examined under the low powers of the microscope. When
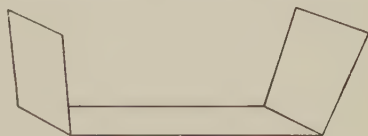
the material is pale in colour, black or tinted paper may with advantage be placed between the cardboard and the slide. Material growing on agar can effectively be studied in surface view by placing a block of agar with the undisturbed fungus on the slide; a lateral view is obtained by cutting a thick slice of agar and laying it on its side. With transparent media in thin layers, it is often possible to make out a good deal without opening the dish, by turning it upside down. If it is necessary to retain for future use a culture from which a specimen has been removed, care must be taken to cut out the latter with a sterilised scalpel; a dish which is wanted again should not be fully uncovered, or its lid placed upon the bench, or turned upside down.

For examination in transmitted light, material may be dipped in 70 or 90 per cent. spirit to remove air, washed and mounted in water, or it may be examined in glacial acetic acid, which has the advantage of ensuring that conidia remain attached. Asci and moist specimens can be examined in water without preliminary treatment.

Material for permanent preparations, to show habit or general characters, should be fixed in 70 per cent. spirit, or in one of the chromacetic mixtures[1]. Such material is usually best mounted in glycerine or glycerine jelly. An excellent method, especially for hyphae and young fructifications growing on agar, is to immerse the fixed material, after washing in water and taking up to 50 per cent. spirit, in equal parts of pure glycerine and aqueous solution of erythrosin. After a few minutes the specimen is washed in 50 per cent. aqueous glycerine which, when the superfluous stain has been removed, may be allowed to concentrate as required. A solution of cotton blue may be similarly employed. As much as possible of the agar is cut away, and the remaining thin slice, with the undisturbed fungus, mounted in glycerine jelly; the agar melts into the warm jelly and a very clear preparation is obtained. It must be emphasised that on no account should material on agar be disturbed at any stage of preparation. It is seldom advisable to take loose hyphae or hand sections of fleshy fungi into balsam; glycerine or glycerine jelly involve much less danger of contraction, but some of the parasitic forms, such as *Epichloë* or *Peronospora*, are sufficiently strengthened by the tissues of their host to make effective balsam mounts; they stain well with safranin and light green.

[1] For formulae of fixatives and stains see pp. 333–6.

In objects so minute as fungal hyphae, or their spore mother cells or spores, cytological methods are required for detailed work, and even these often prove inadequate to elucidate the finer structure of the cell or the behaviour of the nuclei; in particular there is a danger of confusing small nuclei with metaplasmic granules which take up a similar stain.

Fixation. In a very large number of cases the most satisfactory fixative for the detailed study of fungi has proved to be Flemming's strong fluid diluted with an equal quantity of water. Where there is considerable storage of food material, as in the oogonia of *Pyronema*, Merkel's fluid gives more transparent and more readily stainable results, while, in the case of rusts and some other parasites, particularly clear preparations can be obtained with acetic alcohol. Flemming's weak solution, the acetic mixtures, and a number of other fixatives are useful for purposes of comparison; in the case of research material several fixatives should always be tried and alternatives used from time to time.

It is essential that there should be no delay between gathering and fixing material; fungi growing under natural conditions must be fixed on the spot; even if the specimens are carried home on their substratum, normal growth is apt to be prejudiced. The best results are usually obtained during the warmer hours of the day, from noon onwards, or, in some cases, at midnight. Abundant nuclear divisions may be secured at midnight, for example, in various Hymenomycetes. In respect of fungi growing in culture the time of day seems less important, presumably owing to their relatively uniform conditions.

Where a fixing fluid is used that does not contain alcohol, and where the material is not itself saturated with water, air must be pumped out as soon as the pieces of material have been dropped into the fixative. For laboratory purposes a foot pump, such as Hearson's patent air pump, is convenient; for field work a small exhaust syringe can be carried. The pump is attached to a tube passing through a rubber cork (fig. 284), and an exit tube is provided with a clip, which can be quickly opened, allowing the sudden entrance of air, and causing the pieces of material to sink.

For fixation in the field, a box or case fitted with half a dozen bottles or tubes containing fixatives is convenient; a rubber cork should be carried which fits them all and is provided with the

necessary connections for attachment to the syringe. If acetic alcohol is to be used, spirit for washing must be carried.

Everything should be ready for rapid work before the material is gathered; to expedite matters only a few pieces should be picked at a time; these can be put in the fixative and pumped, and others added and pumped again. Small specimens may be fixed whole, larger ones should be cut into blocks about five millimetres square. To avoid delay, adherent particles are better fixed with the fungus and cleaned away under a lens when the material reaches spirit or Calberla's fluid.

After Flemming's fluid, Merkel's fluid, and the chromacetic mixtures, material is washed in running water for six to twelve hours. A convenient washing bottle (fig. 285) has a funnel through which water enters, and an escape tube closed by a piece of fine muslin; this can be used either for objects of ordinary size, or for minute specimens enclosed in muslin bags. After washing,
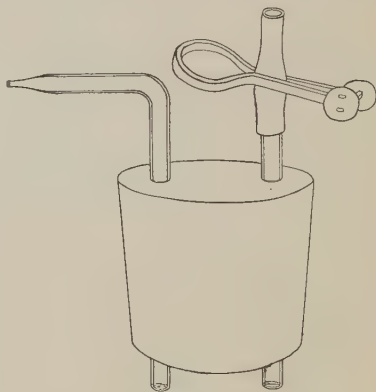
Fig. 284.

the material is placed in 20 per cent. spirit for half an hour or more, and successively in 40, 60 and 80 per cent. spirit for three or more hours each; where nuclear structures are to be studied the strengths of spirit should be increased by 10 per cent. instead of by 20 per cent. From 80 per cent. spirit the material may be transferred for storage to Calberla's fluid, consisting of equal parts of water, absolute alcohol and glycerine, or taken up to absolute alcohol and embedded.

Specimens fixed in acetic alcohol are left in the fixing fluid for fifteen to thirty minutes and well washed in 90 or 95 per cent. spirit; from this they may be transferred to Calberla's fluid or embedded at once.

Preparation of Slides. Material for embedding is selected and, if necessary, cleaned under a lens; it is carried to 90 or 95 per cent. spirit for a few hours and thence to absolute alcohol. After about three hours in this fluid, it is transferred for a similar

length of time to equal parts of alcohol and chloroform and thence
to pure chloroform. Xylol may be similarly used when economy
is an object, but makes some material brittle. Delicate material
is passed through one part of chloroform and three parts of alcohol,
equal parts of alcohol and chloroform, and three parts of chloroform
with one of alcohol before being put into chloroform. Chloroform
is a heavy liquid, and the specimens
as a rule will not sink in it; this
difficulty is overcome by adding a
few shavings of paraffin, which both
push down the material, and, as
they dissolve, reduce the gravity of
the liquid. The chloroform and
paraffin mixture should be left for
some hours at ordinary tempera-
tures, preferably in an uncorked
tube about 3 centimetres high by
2 across; during this period a little
of the chloroform evaporates, the
proportion of paraffin in the mixture
being thereby increased, and further
shavings of paraffin may be added
from time to time. The process is con-
tinued under warmer conditions on
the top of a water-jacketed oven, and
finally for about twenty minutes inside.
The contents of the tube are then
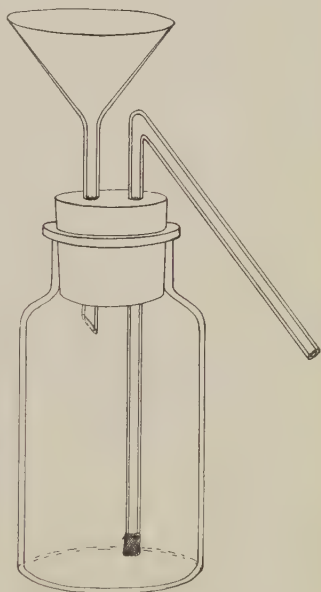
Fig. 285.

emptied into a warm watch glass and left in the oven for another
ten minutes; by this time, if the earlier stages have been sufficiently
prolonged, all sign of chloroform should have disappeared. Mean-
while a stoneware saucer, two inches in diameter, is warmed,
smeared evenly with pure glycerine, placed in the oven and filled
with fresh paraffin; the material is transferred to it with warm
forceps, and the paraffin solidified by holding the saucer over a
dish of cold water, blowing gently on the surface till a film is
formed, and finally immersing the saucer and its contents in the
water. The block of paraffin, when cold, should float out of the
saucer; if it sticks the application of the glycerine has probably
been faulty, and the paraffin may be cut away round the edges or

loosened by cautious warming. A total of half-an-hour in the oven is long enough for small pieces of material; the temperature should be just above the melting point of the paraffin employed. For fungi which are to be sectioned at temperatures of 15° to 20° C., paraffin melting at 52° C., or a mixture of this with paraffin melting at 60°, has proved most satisfactory. The melting point can conveniently be ascertained by putting a drop of liquid paraffin on the bulb of a warmed thermometer, and, as the thermometer cools, noting the temperature of coagulation. Material embedded in paraffin can be kept indefinitely. It is convenient to embed with the material a slip of paper on which the genus and species are written in ink with a number or other symbols indicating the previous treatment.

Very minute objects, for which the numerous transfers between the fixing fluid and paraffin are difficult, may be placed, after washing in water, in 10 per cent. aqueous glycerine; the water is allowed to evaporate in a desiccator, and, when the glycerine is pure, as tested by the addition of a drop of pure glycerine, the material is well washed in absolute alcohol, transferred to 10 per cent. cedar oil in absolute alcohol, and the mixture allowed to evaporate until pure cedar oil remains; shavings of paraffin are then added, first at room temperature, then on the top of the oven, and then inside, and the material is embedded as before, special care being taken to transfer as little cedar oil as possible to the embedding saucer, and two saucers of fresh paraffin being used in succession if required.

The ribbon of microtome sections is now prepared in the usual way, sections being cut from 3μ to 20μ thick according to the objects to be studied and the stain to be used. In reasonably transparent material such cytological stains as Breinl's combination give good results at 10 or 15μ and nuclei may then be studied entire. The ribbons of sections are laid out on white paper with the shiny side down; it is well to avoid as far as possible lifting the rows of sections over each other, either by laying out the first strip of ribbon at the bottom of the paper and starting from the left-hand end to fill the top of the slide, or, if the ribbon is started from the upper edge of the paper, to take first the last cut sections from the right-hand end of the bottom row and place them at the lower edge of the slide. In the case of minute objects it is ad-

visable to take especial pains to lay the sections evenly on the slide; this is most easily done if only the middle two inches of the slide are smeared with albumen mixture and this is covered with three or four drops of water; strips of the ribbon $1\frac{1}{2}$ inches long are then arranged on the slide, the vacant space is filled with lengths of blank ribbon, and the slide is gently warmed till the ribbon lies flat. The superfluous water is drawn off and the slide left in a warm place till dry. Then, and not till then, the slide is warmed sufficiently to allow the albumen to coagulate, attaching the sections, and the slide is placed in the oven for a few minutes to melt the paraffin, and afterwards immersed in a jar of commercial xylol. The xylol may be washed off with 90 or 95 per cent. spirit, and the slide washed at once with water. In our experience the sections, once attached to the slide, can be transferred direct from 90 per cent. spirit to water and from water to spirit without injury to the most delicate structures.

The sequence of the slides should be carefully preserved, either by numbering them with a glass pencil as they are covered with sections, or by subsequently matching the pattern of the sections as seen with the naked eye and numbering on the label. If at any time during these processes sections are lost, so that the sequence of sections on the slide, or from slide to slide, is interrupted, a note to that effect should be made; otherwise an object under the microscope cannot be followed with confidence from one section to another.

When there is much food stored in the structures to be studied it is sometimes desirable to treat the material with gastric juice, which digests the contents of the cytoplasm, leaving the nuclei unaffected. As albumen is destroyed by this treatment the sections must be attached to the slide without its help. The slide is very carefully cleaned, and should not be used unless it is covered by an even film of moisture when breathed upon. Three or four drops of distilled water are then spread over the middle two inches of the slide, the sections are added and the usual procedure followed, very special precautions being taken to dry the slide slowly and thoroughly before placing it in the oven.

Sections of material fixed in an osmic fluid should be bleached to remove the blackening due to this reagent. They may be placed in hydrogen peroxide or in a solution of chlorine in spirit. The

time required depends on the material and can only be ascertained by microscopic examination; twenty minutes is a minimum for hydrogen peroxide, and ten minutes for chlorine. When bleached the sections should be well washed with spirit.

Most of the stains in ordinary employment can be used for fungi; satisfactory results have been given in our experience by the combinations cited below, directions for the preparation of the constituents of which will be found at the end of this chapter. All stains require careful preparation, many need some time in which to ripen, and most should be filtered before use, and may with advantage be filtered again if they have been left standing.

It is advisable to use pipette bottles for absolute alcohol, cedar oil, pure xylol, clove oil and clove oil stains; where the sections are attached to the slide, the latter is shaken almost dry by two or three rapid jerks of the wrist and held in a sloping position while the reagent is applied to the upper end and allowed to run over the sections; if the process is quickly carried out a very small quantity of reagent is sufficient for each slide. Unless the material and stain are so well known that results can be judged under the lower powers of the microscope, it is advisable to mount first in cedar oil, which can be renewed as required by standing the slide edge down in a shallow bath, and not to transfer to balsam till the stain is found to be as good as possible. Sections should never be transferred to balsam direct from clove oil, as this reagent gradually washes out a number of stains.

Safranin and Light Green. For general work, and especially for parasitic fungi when part of the host tissue has to be stained, the sections may be washed with water, placed in safranin for about five minutes, washed in water to remove the surplus stain, washed in spirit, washed in absolute alcohol, transferred to a drop of saturated solution of light green in clove oil, and watched under the microscope till the safranin remains only in the nuclei and in the lignified walls of the host, the walls of the hyphae and the cellulose walls of the host being stained green. The clove oil is then washed away with cedar oil or xylol, and the sections mounted in cedar oil or canada balsam. The stain serves well to differentiate fungal hyphae in the xylem of the host.

Methylene Blue and Erythrosin. A similar procedure with methylene blue followed by saturated solution of erythrosin in

clove oil is also effective, and preferable if much resin is present in the tissues of the host; the nuclei in this combination are stained blue, and the walls of the hyphae red.

If hand sections are stained by either of these methods, they should be left in absolute alcohol for some minutes, and care should be taken to cover the alcohol, so as to prevent the absorption of water from the breath of the operator or otherwise.

Haematoxylin. For microtome sections designed to show general cytological characters, or for the nuclei of undisturbed hyphae on agar, Heidenhain's haematoxylin is satisfactory, and may be followed by light green, erythrosin or orange G in clove oil. The sections are washed in water, left in the mordant for from twenty minutes to two hours, washed in water, placed in haematoxylin for one to twenty-four hours, and again well washed with water before the stain is washed out under the microscope. The best mordant in our experience is the liquor ferri of Benda; if it is not obtainable iron alum solution is an effective substitute. For washing out a Petri dish is convenient, containing a supply of the mordant diluted with water to the colour of pale sherry and acidulated with a drop or two of acetic acid; if the time of staining has been short, the sections should merely be dipped in the diluted mordant and washed in water before examination; if staining has been prolonged they may remain in the mordant for several minutes and be examined in it under the microscope, or a stronger solution of the mordant may be used; as a rule rapid washing out increases the sharpness of the stain. When the stain is satisfactory the mordant is washed off and the slide placed for about five minutes in running tap water, the faint alkalinity of which neutralises the acidity of the mordant. The slide is then taken through spirit and absolute alcohol to clove oil, or, if a counter-stain is not required, to cedar oil or xylol.

Safranin, Gentian Violet and Orange G. Flemming's triple stain, or gentian violet and orange G alone, are also useful stains. The sections are placed in safranin for three to twelve hours, washed with water to remove the surplus stain, washed with spirit, examined, further washed out, if necessary with acid alcohol, washed with spirit, washed with water, placed in gentian violet for thirty minutes, and again washed with water; they may then be covered for a few seconds with an aqueous solution of

orange G and taken up to cedar oil, or they may be taken at once through spirit and absolute alcohol to clove oil in which orange G has been dissolved; in either case the passage through spirit and absolute alcohol should be rapid, or much of the stain will be lost.

Safranin, Polychrome Methylene Blue and Orange Tannin. If the nuclei are reasonably large by far the best cytological stain in our experience is the combination originated by Breinl. The slide is placed for fifteen minutes in a solution of iodine and potassium iodide in spirit, washed with water, transferred for thirty minutes or longer to equal parts of aqueous and of alcoholic safranin, washed with water, placed for ten minutes in polychrome methylene blue, and again washed with water; it is then dipped into orange tannin and in this fluid examined under the microscope till the orange has displaced the blue in the cytoplasm, washed with water, well washed with 90 or 95 per cent. spirit, quickly transferred through absolute alcohol to aniline oil, and again watched under the microscope till any excess of blue is removed. In our experience pure aniline oil does not act on the stain, the required reaction being presumably due to an impurity in the commercial substance. Finally the aniline oil is replaced by cedar oil and the sections covered in readiness for a preliminary examination under high powers, before permanent mounting in balsam. In good preparations the spireme is brilliant blue-black, the cytoplasm faintly yellow, and the chromosomes of the meiotic metaphase bright red. The stain is rather difficult to use and failures in its first application are inevitable, but a successful preparation, when obtained, will be found to justify perseverance; as it is very transparent sections as thick as 15μ can be used.

Congo Red. Congo red is a valuable counter-stain for rusts after haematoxylin, since it colours the walls of the parasite but not of the host; it acts excellently after fixation with acetic alcohol, and, if the sections are well washed before transfer to balsam, will remain bright for as long as twenty years.

CULTURE MEDIA

1. Potato Agar.

   About 250 grm. of potatoes are peeled, cut into small pieces and boiled for about an hour. The extract is allowed to cool and settle; as much as possible of the clear, supernatant liquor is poured off and made up to 1000 c.c. with tap water. It is placed in a flask with 25 grm. of agar and sterilised. The quantity is sufficient for about three dozen Petri dishes.

2. Dung Agar.

   About 1000 grm. of horse, cow, or rabbit dung are soaked in cold water for three days, the liquid is poured off and diluted till the colour of straw; 2·5 grm. of agar are added for every 100 c.c. of the diluted fluid.

3. Pea Agar.

   400 dried peas are boiled for an hour, the liquid is poured off, made up to 1000 c.c. and 25 grm. of agar are added.

4. Prune Agar.

   25 prunes are boiled for an hour, the liquid is poured off, and made up to 1000 c.c.; 400 grm. cane sugar and 50 grm. agar are added.

5. Claussen's Medium[1].

   Inner dish.

Potassium dihydrogen phosphate, KH_2PO_4 ...	0·05	grm.
Ammonium nitrate, NH_4NO_3	0·05	grm.
Magnesium sulphate, $MgSO_4$, $7H_2O$	0·02	grm.
Ferrous phosphate, $Fe_3(PO_4)_2$	0·001	grm.
Agar	3·0	grm.
Distilled water	100·0	c.c.
Inulin	2·0	grm.

   Outer dish.

   As above, but without inulin.

6. Barnes' Medium.

Tripotassium phosphate, K_3PO_4	0·1 grm.
Ammonium nitrate, NH_4NO_3	0·1 grm.
Potassium nitrate, KNO_3	0·1 grm.
Glucose	0·1 grm.
Agar	2·5 grm.
Distilled water	100·0 c.c.

FIXATIVES

1. Flemming's fluid, strong:

1 % chromic acid in water...	75 c.c.
Glacial acetic acid	5 c.c.
2 % osmic acid in water	20 c.c.

   Flemming's strong fluid diluted with an equal volume of water (Flemming $\frac{1}{2}$ S.) is to be preferred for delicate objects.

[1] Claussen, 1912.

2. Flemming's fluid, weak:

1 % chromic acid in water...	25 c.c.
1 % acetic acid in water	10 c.c.
1 % osmic acid in water	10 c.c.
Water	55 c.c.

3. Merkel's fluid:

1 % chromic acid in water...	25 c.c.
1 % platinic chloride in water	25 c.c.
Water...	150 c.c.

4. Chromacetic mixture, strong:

1 % chromic acid in water...	140 c.c.
Glacial acetic acid	1 c.c.

5. Chromacetic mixture, weak:

1 % chromic acid in water...	140 c.c.
Glacial acetic acid	1 c.c.
Water...	60 c.c.

6. Acetic alcohol:

Glacial acetic acid	20 or 25 c.c.
Absolute alcohol	80 or 75 c.c.

ALBUMEN

White of egg....	50 c.c.
Glycerine	50 c.c.
Sodium salicylate	1 grm.

An egg is cautiously broken, the white is separated from the yolk, the sodium salicylate is dissolved in a very little water, the other ingredients are added and the whole well beaten and filtered.

GASTRIC JUICE

Benger's liquor pepticus: a few drops in 0·2 % hydrochloric acid.

STAINS

1. Safranin, Polychrome methylene blue and Orange tannin (Breinl's stain):

Safranin O, saturated aqueous solution	50 c.c.
safranin, alcohol soluble, saturated solution in absolute alcohol	50 c.c.
aniline oil	a few drops.

The mixture is improved by keeping for three months to ripen.

Polychrome methylene blue	7 grm.
sodium carbonate	0·5 grm.
water	100 c.c.

This also is improved by keeping; ripening may be accelerated in an incubator.

Orange tannin: may be used as supplied by Grübler.

Iodine	...	...	...	...	...	...	1 grm.
potassium iodide		...	...	...	...	1 grm.
80 % spirit	...	...	...	...	...	100 c.c.

2. Safranin, Gentian violet and Orange G (Flemming's triple stain):

Safranin, alcohol soluble, saturated alcoholic

solution	...	...	...	...	...	50 c.c.
water	...	...	...	...	...	50 c.c.
aniline oil	...	...	...	...	...	3 drops.
Gentian violet	...	...	...	...	...	1 grm.
20 % spirit	...	...	...	...	...	100 c.c.

Orange G: saturated aqueous solution *or* saturated solution in clove oil.

3. Iron haematoxylin:

| Haematoxylin | ... | ... | ... | ... | ... | 1 grm. |
| absolute alcohol | | ... | ... | ... | ... | 10 c.c. |

This stock solution is ripened by keeping for some months or by the addition of a drop of hydrogen peroxide; 5 c.c. are then made up to 100 c.c. with water, and a drop of the mordant is added before use.

| Iron alum | ... | ... | ... | ... | ... | 4 grm. |
| warm distilled water | ... | ... | ... | ... | 100 c.c. |

The spirit is added after the iron alum is dissolved.

Liquor ferri of Benda:

| the liquor ferri of the German Pharmacopoeia[1] | 20 c.c. |
| water | ... | ... | ... | ... | ... | 80 c.c. |

4. Congo red:

Congo red	...	...	...	...	...	1 grm.
water	...	...	...	...	...	100 c.c.
ammonia	...	...	...	...	...	a few drops.

or Saturated solution of congo red in clove oil.

5. Safranin and light green:

Safranin: either of the methods of preparation described above; that for Breinl's stain is on the whole the best.

Light green: saturated solution in clove oil.

Saturated solutions are conveniently prepared by covering the bottom of a bottle with the dry stain and filling with clove oil; the saturated solution can be decanted off from time to time and filtered if necessary, and the bottle refilled till all the stain is dissolved.

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[1] The liquor ferri of the British Pharmacopoeia is a different compound and has not been found effective, neither has a solution made up with pure chemicals from the German formula.

6. Methylene blue and Erythrosin:

Methylene blue	...	...	...	...	...	1 grm.
water	...	...	...	...	...	100 c.c.

Erythrosin: saturated solution in clove oil.

7. Cotton blue:

Saturated solution of cotton blue in spirit					...	10 c.c.
pure glycerine	...	...	...	...	...	10 c.c.
water ...	...	...	...	...	...	80 c.c.

The material is left in the stain for about three days during which some of the water and spirit evaporate; it is then washed in dilute glycerine.

8. Erythrosin Glycerine:

Saturated aqueous solution of erythrosin					...	50 c.c.
pure glycerine	...	...	...	...	...	50 c.c.

The material is left in the stain for a few minutes, then washed in 50 % glycerine. With a more dilute stain the procedure for cotton blue is appropriate.

CLEANING SLIDES AND COVERSLIPS

Both slides and coverslips should be cleaned before use; in view of the greater delicacy of the coverslips they should be treated separately.

1. The slides or coverslips are placed in hot 5 % solution of potassium bichromate in water and a little concentrated sulphuric acid is added at intervals of 5 or 10 minutes; the mixture is kept bubbling for not less than 30 minutes. The slides or coverslips are then washed in running water for 12 hours, washed in distilled water and kept till required in 95 % spirit.

2. Coverslips are usually sufficiently cleaned by keeping for about a week in 95 % spirit to which a few drops of hydrochloric acid have been added. They may then be washed in water or spirit and transferred to 95 % spirit till needed, or may be washed in spirit and used at once.

3. Coverslips are quickly and effectively cleaned by rubbing with soap and water between the thumb and finger, washing in water and washing in spirit.

BLEACHING AGENTS

1. Hydrogen peroxide:

Hydrogen peroxide, 20 vol. solution		...	...		40 c.c.
60 or 80 per cent. spirit	...	...	...		60 c.c.

2. Chlorine:

Potassium chloride ...	...	...	...		... a few crystals
concentrated hydrochloric acid		...	...		1 drop
60 per cent. spirit	...	...	...		... 60 to 100 c.c.

The spirit is added when a green colour indicates the evolution of chlorine. Prolonged washing in spirit is required after this reagent.

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A glossary has not been prepared for this volume, but the page on which the definition of a technical term will be found is shown in the index in clarendon type, and the same method is used for indicating the principal reference to a family or genus. Names of authors will be found in the bibliography on p. 337.

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